THE AMPHIPOD GENUS *PARAMOERA* MIERS (GAMMARIDEA: EUSIROIDEA: PONTOGENEIIDAE) IN THE EASTERN NORTH PACIFIC

Craig P. Staude[1]

ABSTRACT

Six new species and one subspecies of the amphipod genus *Paramoera* are described from the eastern North Pacific, bringing the total to 12 congeneric species in this region. *Paramoera serrata,* new species, *P. serrata escofetae,* new subspecies, *P. suchaneki,* new species, and *P. bousfieldi,* new species, form the unresolved grade "*Paramoera*" with the type species *P. australis* Miers, 1875 and most other *Paramoera* of the Southern Hemisphere. The new subgenus *Moanamoera* is erected to receive the three Hawaiian species previously described by J. L. Barnard (1977). *Paramoera leucophthalma,* new species and *P. crassicauda,* new species, are placed in the new subgenus *Humilomoera. Rhithromoera,* new subgenus, is erected to receive *Paramoera carlottensis* Bousfield, 1958 and *P. bucki,* new species. Members of these more advanced subgenera of the North Pacific exhibit some reduction in morphological characters and are found mostly in waters of reduced salinity. A regional key to species is presented, and distributional and ecological information is given for each species. The systematic relationship among the regional species is contrasted with the marine congeners of the Southern Hemisphere. Evolutionary and biogeographic trends are discussed.

INTRODUCTION

Amphipods of the genus *Paramoera* are common inhabitants of marine cobble and gravel beaches along the western coast of North America. Some species are estuarine, entering the tidal portion of streams. They attain high population densities and provide a significant prey resource to fishes (Staude, 1986). Yet despite their importance, these amphipods are poorly known.

Our first knowledge of the amphipod genus *Paramoera* was prompted by an international expedition to observe the transit of Venus in 1874 and 1875. The United States, Germany, and Great Britain each established astronomical observatories on the remote southern island of Kerguelen. The Rev. A. E. Eaton, naturalist of the British expedition, collected numerous specimens of flora and fauna from the area, including those destined to become the type specimens of *Paramoera* .

Miers (1875a) formally described these specimens as *Paramoera australis*, and diagnosed the genus on the basis of four characters: antenna 1 being slightly longer than antenna 2, gnathopods being subequal and well developed, uropod 3 ("posterior pleopoda") having a rudimentary inner ramus, and the telson being cleft nearly to its base.

The inadequacy of this descripton soon became apparent. One month later, Miers (1875b) attempted to retract his original designation. He moved *australis* to the genus *Atylus*, admitting that he had been mistaken about the condition of uropod 3. He further suggested (Miers, 1879) that a new

genus be erected to receive *Atylus australis* as well as *Amphitoe fissicauda* of Dana (1852) and *Atylus austrinus* of Bate (1862), but he did not formally establish such a genus. This new group lacked the dorsal carinations of *Atylus*, and was grossly similar to the genus *Melita*, but lacked an obvious accessory flagellum.

Miers (1879) still entertained the thought that his genus name of *Paramoera* could be applied to species with reduced uropods, but by 1885 he had become resigned to its demise. In a letter cited by Stebbing (1888) Miers commented, "I suppose the genus *Paramoera* will hardly stand."

Stebbing's report on the Challenger Expedition (1888) decreed *Paramoera* to be "scientifically unsuitable" and unrevivable due to the inaccuracies of the original diagnosis. He erected the genus *Atyloides* to receive the orphaned species, *Paramoera australis*. But eighteen years later Stebbing reversed his decision. In his authoritative monograph of 1906 Stebbing reestablished the name *Paramoera,* and provided a revised diagnosis. Yet in that same work he synonymized and submerged the type species, *Paramoera australis* Miers, with *P. austrina* (Bate). Under the present rules of nomenclature, *P. autralis* Miers 1875 remains the legitimate type species of the genus *Paramoera* (confirmed by Dr. Melville of the International Commission of Zoological Nomenclature via personal communication with Dr. M. Thurston, 1985).

Another blow was delt by Schellenberg in 1931 who synonymized twenty taxa of earlier authors under the name *Paramoera fissicauda* (Dana). Most of these sweeping changes were reversed by later authors (K.H. Barnard, 1932; Thurston, 1972; Bellan-Santini and Ledoyer, 1974).

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[1]Friday Harbor Laboratories, University of Washington, Friday Harbor, WA, 98250, USA

This shuffling of nomenclature and the inadequacy of most early descriptions have left this group in a crippling state of confusion. While working on subantarctic species of *Paramoera* , J.L. Barnard (1972a) complained, "I am yet unable to turn to the literature and easily make some sense of the species without painstaking cross-referencing that often terminates blindly." He rediagnosed the genus (J.L. Barnard, 1972b), but concluded that "the identity of various species of *Paramoera* is so confounded presently that I cannot properly evaluate variables within that genus." Bellan-Santini and Ledoyer (1974), in their comprehensive review of *Paramoera*, concurred that a revision is necessary.

Throughout this century the number of species of *Paramoera* has grown to more than forty. Marine and freshwater species were discovered in the vicinity of Japan and Korea (Tattersall, 1922; Stephensen, 1944; Bulycheva, 1952; Ueno, 1933, 1971a, 1971b), and three species were reported from the Pacific coast of North America (J.L. Barnard, 1952; Bousfield, 1958). When J.L. Barnard added three unusual new species from Hawaii in 1977 he suggested that they might qualify as a new subgenus of *Paramoera*, but he hesitated to erect this taxon because of the "taxonomic instability" of many pontogeneiid genera.

In 1982 J.L. Barnard and G.S. Karaman began to carve up this unwieldy composite of species into new allied genera. Japanese species with sinusoid cephalic lobes were assigned to *Relictomoera*, while those with sternal gills became *Sternomoera*. But even this recent revision is problematic. Hirayama (1990) has urged the submergence of the genus *Relictomoera*, claiming that the cephalic lobes of these species are not unusual for the genus *Paramoera*. The need is apparent for further investigation of these western North Pacific species at the level of genus or subgenus.

A major impediment to the resolution of *Paramoera* (sensu lato) is our incomplete knowledge of the type specimens. Miers' original description (1875a) and his further elaboration in 1879 fail to provide an adequate basis for comparison of the many species which have since been discovered around the world. In 1974 Thurston urged the reexamination of this and other early species. He has since succeeded in resurrecting Mier's specimens which were entombed in the British Museum, and has begun to redescribe and refigure both *Paramoera australis* and *P. austrina* (Thurston, pers. comm.). The final disposition of *Paramoera* and its allied genera will depend on further developments in this area.

Until recently (Staude 1987), only 3 species of *Paramoera* were recognized in the eastern North Pacific (Bousfield 1958, Barnard, 1975). The environmental concern of the last three decades prompted numerous baseline surveys of marine invertebrates (e.g., Armstrong et al., 1976; Nyblade, 1979), uncovering additional species. A closer examination of museum collections has revealed still other undescribed species of *Paramoera* .

This paper formally describes 6 new species (and one new subspecies) of *Paramoera* from the west coast of North America, making a total of 9 for this region and 3 from the adjacent Hawaiian Islands. These new discoveries suggest three or more subgeneric groups.

METHODS

The material examined in this study was collected from 45 geographic localities from the Pribilof Islands to Ensenada, Mexico, and was made available from numerous sources.

The names of collectors or the institutions where material is housed are abbreviated as defined in Table 1.

TABLE 1. Collection abbreviations

AE = Anamaria Escofet, Centro de Invest. Cientificas, Ensenada, Baja California, Mexico

AHF = Allan Hancock Foundation, Los Angeles, CA (now at the L.A. County Museum)

AR = Anthony Roth, Nautilus Associates, Port Angeles, WA

BM = Dr. Bruce Miller, University of Washington

CAS = California Acad. of Sciences, San Francisco, CA

CFN = Dr. Carl F. Nyblade, University of Washington

CPS = author

CL = Dr. Colin Levings, Pacific Environmental Inst., Vancouver, BC

CS = Charles A. Simenstad, University of Washington

ELB = Dr. E.L. Bousfield, National Museums of Canada

FGH = Dr. F. G. Howarth, Bishop Museum, Hawaii

FR = Fahmida Rafi, National Museums of Canada

G and S = Ghelardi and Sikora, University of California

JDC = John D. Chapman, University of California

JLB = Dr. J.L. Barnard, U.S. National Museum

JLM = Dr. John L. Mohr, Univ. of Southern California

JTC = Dr. John T. Carlton, California Acad. of Sciences

JWA = Dr. John W. Armstrong, Univ. of Washington

LACM = Natural Hist. Museum of Los Angeles County

METRO = Municipality of Metropolitan Seattle, WA

MLM = Dr. Michael L. Murphy, Nat'l. Marine Fish. Service, Auke Bay, AK

NMC = National Museums of Canada (now Canadian Museum of Nature)

NOAA = National Oceanic and Atmos. Admin. (Puget Sound MESA Program)

PS = Mr. Patrick Shaw, Univ. of British Columbia

PNS = Dr. Peter N. Slattery, Moss Landing Lab., CA

RJL = Ronald J. Long, Simon Fraser University, Vancouver, BC

RJM = Dr. Robert J. Menzies, Univ. of Southern Calif.

SAM = South African Museum

SJS = Sarah J. Staude, author's assistant

THS = Dr. Thomas H. Suchanek, Univ. of Washington

USNM = U. S. National Museum (Natural History)

The major portion of the loan material was borrowed from the National Museum of Natural Sciences, National Museums of Canada. Collection information for these specimens was reported by Bousfield (1957 and 1963),

Bousfield and Hubbard (1968), and Bousfield and Jarrett (1981).

Many specimens were personally (Staude, 1986) collected by means of live (350 μm) and dead (500 μm) sieving of sediment cores, by 0.3 m hand-towed plankton net (330 μm mesh), and by a suction sampler or coarse forceps. Qualitative samples were also taken by a "bucket swirl" technique, in which small amounts of sediment were agitated in a bucket of clean seawater, the bucket swirled, and the water decanted through a sieve. Scuba collections of sediment cores were made at Cape Beale, B.C., and at Deadman Bay, Washington.

Specimens of the author's collection were fixed in 10% buffered formalin, and preserved in 70% ethanol with 5% glycerol. Selected specimens were stained with lignin pink or methylene blue, dissected in a glycerol/ethanol (1:1) solution and mounted in 96% glycerol with a ringed coverslip. Illustrations were made by camera lucida with both dissecting and compound microscopes. The specimens were optically "uncurled" and body parts optically repositioned to provide a uniform figure. Body length was measured from the tip of the rostrum to the base of the telson.

Abbreviations of illustrations are defined in Table 2.

TABLE 2. Abbreviations used in figures

A1 = antenna 1	MX1 = maxilla 1
A2 = antenna 2	MX2 = maxilla 2
C2 = coxa 2	MXPD = maxilliped
EP3 = epimeron 3	PL2 = pleopod 2
GC = gland cone	P4 = peraeopod 4
GN1 = gnathopod 1	P7,2 = P7, segment 2
GN2 = gnathopod 2	RT = right
LFT = left	U1 = uropod 1
LL = lower lip	U2 = uropod 2
LM = lacinia mobilis	U3 = uropod 3
m = male	T = telson
MD = mandible	

The information presented here is condensed from a more rigorous examination contained in my dissertation (Staude, 1986). That work includes full descriptions of female holotypes and male paratypes for each new species, and contains the detailed phenetic and cladistic analyses on which I base the new subgenera. The phenetic clustering was performed using the CLUSTAN program at the University of Washington Academic Computing Center utilizing the group averaging method (Sneath and Sokal, 1973). The cladistic analysis was done on a microcomputer using various routines of the program PHYLIP (Felsenstein, 1984, 1985). The fifty-two characters used in these analyses were presented in my dissertation (Staude, 1986). For the purpose of these phyletic comparisons, the group ancestor was in part patterned after *Paramoera bidentata* K.H. Barnard, 1932, and the "type" concept was based on personal communication and

unpublished materials from Dr. Michael Thurston, who has reexamined the type material of the genus *Paramoera*.

Throughout this paper there are references to a publication in press (e.g., "*Paramoera serrata* Staude (in press)") that were originally cited (Staude, 1987) in an identification guide to invertebrates (Kozloff, 1987). Unfortunately, that paper never appeared in print due to funding cuts and policy changes at the supporting institution.

SYSTEMATICS

Paramoera Miers, 1875

Paramoera Miers, 1875a: 75.--Stebbing, 1906: 363.-- Schellenberg, 1929: 280.-- J. L. Barnard, 1969a: 227.-- Barnard, 1972b: 184-186.--Barnard, 1977: 275-278.
Stebbingia Pfeffer, 1888 (fide J. L. Barnard, 1969a)
Atyloides Stebbing, 1888.
Aucklandia Walker, 1908 (fide J. L. Barnard, 1969a)

Type species. *Paramoera australis* Miers, 1875.

Diagnosis. Rostrum vestigial or absent; antenna 1 usually longer than antenna 2; accessory flagellum 1-segmented, scale-like, with 2 long apical setae and a shorter seta to either side; gland cone projecting ventrally, bearing spines or setae; discoid calceoli present in male.

Upper lip symmetrical and evenly rounded; mandibular incisor with 6 teeth, left lacinia mobilis with 5 teeth, right lacinia with 2-3 major teeth, with a blunt tooth at the base of the mandibular palp; segments 2 and 3 of mandibular palp subequal in length; lower lip with inner lobes indistinct or absent; inner plates of maxilla 1 and 2 generally with numerous plumose setae (reduced in apomorphic subgenera), setae of maxilla 2 in a submarginal diagonal row; inner plate of maxilliped with 3 stout apical spine teeth.

Coxae 1-4 without articulated spines along the posterior margins; gnathopods subchelate (not eusirid), with oblique palms, propodus with groups of finely pectinate comb-setae in parallel arrangements along the ventral, medial, and anteromedial margins; carpus of gnathopod 2 lengthened in female (often exceeding the length of the propodus).

Lobes of telson rarely fused more than half its length, with prominent setae or spines near the apices.

Relationships. *Paramoera* differs from *Accedomoera* J. L. Barnard (1964) in the smaller rostrum, the ornamentation of the accessory flagellum, the absence of distinct inner lobes on the lower lip, the more setose maxillae, the absence of spines along the posterior margins of coxae 1-3, the more uniform allignment of gnathopod setae, and the ornamentation of the apices of the telson. It differs from *Pontogeneia* Boeck (1871) by the shorter rostrum, the presence of an accessory flagellum, the ventrally extended (ornamented) gland cone, the longer article 3 of the mandibular palp, the absence of distinct inner lobes on the lower lip, the more setose maxillae

(exceptional subgenera), the absence of spines from the posterior margins of coxae 1-3, the more uniform allignment of the gnathopod setae, and the ornamentation of the apices of the telson. Differing from *Gondogeneia* J. L. Barnard (1972b) by the shorter rostrum, the longer antenna 1, the ventrally extended (ornamented) gland cone, the broader and more setose inner plate of maxilla 1, the greater setosity of maxilla 2 (exceptional subgenera), the more uniform allignment of the gnathopod setae, and the longer basal segments of peraeopods 5-7. Differing from *Tethygeneia* J. L. Barnard (1972b) by the shorter rostrum, the structure of the accessory flagellum, the ventrally extended gland cone, the longer segment 3 of the mandibular palp, the more slender palp of maxilla 1, the more setose maxillae (exceptional subgenera), the more uniform allignment of the gnathopod setae, and by the ornamentation of the apices of the telson. Differing from *Nasageneia* Barnard & Karaman (1982) by the shorter rostrum, the presence of an accessory flagellum, the ventrally extended gland cone, the longer segment 3 of the mandibular palp, the less serrate epimeron 3, and the ornamentation of the apices of the telson. Differing from *Pontogeneiella* Schellenberg (1929) by the shorter rostrum, the presence of an accessory flagellum, the ventrally extended gland cone, the absence of inner lobes from the lower lips, the absence of spines from the posterior margin of coxae 1-3, and the lesser fusion of the telson lobes. Differing from *Antarctogeneia* Thurston (1974) by the presence of an accessory flagellum, the longer segment 3 of the mandibular palp, the absence of inner lobes from the lower lip, the unexpanded coxa 1, the structure of the peraeopod dactyls,

and the less serrate epimeron 3. Differing from *Atyoella* Schellenberg (1929) by the unproduced epistome and the absence of inner lobes from the lower lip. Differing from *Atylopsis* Stebbing (1888) by the absence of inner lobes from the lower lip, the more setose maxillae, and the lesser fusion of the telson lobes. Differing from *Schraderia* Pfeffer (1888) by the more robust (non-linear) gnathopods and the less serrate epimera. Differing from *Apherusa* Walker (1891) by the longer first antenna, the presence of an accessory flagellum, and the presence of calceoli in the male. Differing from *Djerboa* Chevreux (1906) by the more robust (non-linear) gnathopods and the absence of an accessory spine from the dactyls of the peraeopods. Differing from *Awacaris* Ueno (1971c) by the presence of eyes, the more typical mandibular incisor, the typical (unreduced) palp of maxilla 1, and the more uniform ornamentation of uropod 3.

Component groups

The genus *Paramoera* encompasses the grade "*Paramoera* " (the type specimen and its closest relatives, including subgenera that are presently unresolved) and the subgenera *P. (Moanamoera)*, new subgenus, *P. (Humilomoera)* new subgenus, and *P. (Rhithromoera)*, new subgenus.

The diagnosis and composition of this genus are provisional. Subsequent revision of antiboreal species (including the type species) will provide further resolution. The genera *Paramoerella* Ruffo (1974), *Pseudomoera* Schellenberg (1929), *Relictomoera* Barnard & Karaman (1982; see also Hirayama 1990), and *Sternomoera* Barnard & Karaman (1982) are candidates for future designation as subgenera.

Key to *Paramoera* of the eastern North Pacific (adults of both sexes)

1. Head with an acute notch or cleft (inferior antennal sinus) separating the lateral lobe and post-
   antennal lobe; eye larger than 1/2 the depth of the lateral lobe of the head . . . . 2.

---Head with a smoothly curved or quadrate concavity separating the lateral lobe and postantennal
   lobe; eye not larger than 1/2 the depth of the lateral lobe   . . . . 7.

2. Head with a slight cleft separating the lateral lobe and postantennal lobe; gland cone with a single
   short seta; gnathopod 2 of female with carpus more than 25% longer than propodus; uropod 3 with-
   out plumose setae . . . . *Paramoera (Paramoera) bousfieldi* (p. 78)

---Head with a moderate to deep notch or cleft separating the lateral lobe and postantennal lobe; gland
   cone with 1-4 long setae or with stout spines; gnathopod 2 of female with carpus not more than
   25% longer than propodus; uropod 3 with plumose setae (these sometimes reduced and hidden in
   lateral view) . . . . 3.

3. Gland cone with 1-2 stout spines (plus a seta in female); segment 3 of antenna 2 with dorso-distal
   spine; segment 6 of peraeopod 4 with posterior row of spines in groups of 2-3; inner ramus of uro-
   pod 2 with subapical spine larger than proximal spines . . . . *P. (P.) columbiana* (p. 77)

---Gland cone with setae only; segment 3 of antenna 2 without a distodorsal spine; segment 6 of per-aeopod 4 with a posterior row of single spines (+ small setae); inner ramus of uropod 2 with sub-apical spine not larger than proximal spines . . . . 4.

4. Segment 6 of peraeopod 4 with more than 4 spines in the posterior row; posterior margin of epimer-on 3 with more than 3 small posterior notches; outer ramus of uropod 2 longer than inner ramus. .
. . . . *P. (P.) suchaneki* (p. 73)
---Segment 6 of peraeopod 4 with not more than 4 spines in the posterior row; posterior margin of epi-meron 3 with 2 small notches; outer ramus of uropod 2 shorter than inner ramus . . . . 5.

5. Head with a shallow cleft separating the lateral lobe and postantennal lobe; segments 1 and 2 of an-tenna 1 with about 4 groups of long setae along the ventral margins; gland cone of antenna 2 with one long and one short seta . . . . *P. (P.) mohri* (p. 68)

---Head with a deep cleft separating the lateral lobe and postantennal lobe; segments 1 and 2 of antenna 1 with 5 or more groups of long setae along the ventral margins; gland cone of antenna 2 with 4-6 long setae. . . . . 6.

6. Segment 6 of peraeopod 4 with 3 spines in the posterior row; segment 2 of peraeopod 7 with dist-inct posterior serration; urosomite 3 with a distinct dorsal boss (Washington to central California). .
. . . . *P. (P.) serrata* (p. 69)
---Segment 6 of peraeopod 4 with 5 spines in the posterior row; segment 2 of peraeopod 7 without obvious posterior serration; urosomite 3 without a distinct dorsal boss (Baja California). . . . .
. . . . *P. (P.) serrata escofetae* (p. 70)

7. Antenna 1 much longer than antenna 2; inner plate of maxilla 1 with about 4 plumose setae; epi-meron 2 with posteroventral corner quadrate or obtusely angled; uropod 3 without plumose setae (Alaska to Washington) . . . . 8.
---Antenna 1 not much longer than antenna 2; inner plate of maxilla with about 10 plumose setae; epi-meron 2 with posteroventral corner acutely angled; uropod 3 with plumose setae (Hawaiian Islands)
. . . . (*Moanamoera*, n. s.-g.) 11.

8. Head with a deep concavity (inferior antennal sinus) between the lateral lobe and postantennal lobe; gland cone with 1-2 crooked spines; propodus of gnathopods about twice as long as wide; gnatho-pod 2 of female with carpus shorter than propodus; peraeopods 5-7 with carpus slightly longer than propodus; each apex of telson with 3-4 setae . . . . (*Rhithromoera*, n. s.-g.) 9.

---Head with a shallow concavity (inferior antennal sinus) between the lateral lobe and postantennal lobe; gland cone with a single small seta; propodus of gnathopods ,more than twice as longe as wide; gnathopod 2 of female with carpus not shorter than propodus; peraeopods 5-7 with carpus shorter than propodus; each apex of telson with less than 3 setae . . . *(Humilomoera,* n. s.-g.) 10.

9. Eye about 1/3 the depth of the lateral lobe of head; propodus of gnathopods widest proximal to their midpoint; gills absent from peraeopod 7; peduncle of uropod 1 with more than 10 spines in the dorsolateral row, and with an isolated distoventral spine. . . . . *P. (R.) bucki* (p. 91)

---Eye about half the depth of the lateral lobe; propodus of gnathopods widest at or beyond their midpoint; gills present on peraeopod 7; peduncle of uropod 1 with less than 10 spines in the dorso-lateral row, lacking an isolated distoventral spine . . . . *P. (R.) carlottensis* (p. 90)

10. Eyes light; segment 1 of antenna 1 with a distoventral spine; uropod 3 with rami much longer than peduncle; telson fused less than half its length . . . . *P. (H.) leucophthalma* (p. 84)

---Eyes dark; segment 1 of antenna 1 with setae only; uropod 3 with rami longer than the peduncle; telson fused more than half its length .. . . *P. (H.) crassicauda* .(p. 84)

11. Eyes entirely absent; peraeopods elongate (combined length of segments 3-7 of peraeopod 7 more than twice the length of segment 2); uropod 3 with rami about twice the length of the peduncle (hypogean, Island of Hawaii) . . . . *P. (M.) lokowai* (p. 82)

---Eyes present (occasionally reduced to a few ommatidia); peraeopods not elongate (combined length of segments 3-7 not more than twice the length of segment 2); uropod 3 with rami less than twice the length of the peduncle . . . . 12.

12. Posterior margins of epimera with 1-3 spines; posteroventral corner of epimeron 2 produced as an acute tooth; telson fused about 25% of its length, its apices tapered and faintly notched (lava ponds, Island of Hawaii) . . . . *P. (M.) paakai* (p. 82)

---Posterior margins of epimera with 2-3 setae; posteroventral corner of epimeron 2 not produced, posterior and ventral margins meeting at about 75 degrees; telson fused only at its base, its apices broad and deeply notched (cave pools, Island of Maui) . . . . *P. (M.) rua* (p. 82)

"Paramoera" unresolved grade

A group of unresolved subgenera close to the form of *Paramoera australis* Miers, 1875, type species of the genus *Paramoera* Miers

Working diagnosis. Rostrum unproduced; lateral cephalic lobe mammiliform; inferior antennal sinus with a cleft. Eye large, ovate to reniform, and pigmented.

Antennae of moderate length, antenna 1 usually longer than antenna 2, peduncular segments of antenna 1 progessively shorter, segment 1 shorter than the head; accessory flagellum 1-segmented, scale-like; ventromedial setae of peduncles long; gland cone usually with multiple setae or spines; calceoli usually present on male only.

Upper lip entire and rounded; epistome unproduced. Molar triturative, oval; palp with segments 2 and 3 subequal in length. Lower lip without distinct inner lobes.

Maxilla 1: inner plate with 8-15 plumose setae; outer plate with about 10 pectinate spines; palp long, segment 1

short. Maxilla 2: inner plate with 6-15 plumose setae in a diagonal row across the inner face. Maxilliped: inner plate about as long as outer, outer plate with more than 5 medial spine teeth; palp of 4 segments, segment 1 not laterally extended, segment 3 unlobed, segment 4 shorter than segment 3, segment 4 not spinose (but with small distal setae) along the inferior margin, ungiform, with nail.

Coxae 1-3 ordinary, a little longer than wide, sparsely setose, rarely with a developed spine or tooth at the posteroventral corner; coxa 4 with posterior lobe, excavate; anterior lobe of coxa 6 variously produced, ventral margin of coxa 6 rarely with spines (usually with setae only).

Gnathopods moderate, with subchelate oblique palm; segment 5 of gnathopod 2 rarely longer than segment 6, gnathopod 2 of males occasionally with extremely oblique palm, palm often with more than 4 barb spines in the outer row.

Dactyls of peraeopods 3-7 smooth or minutely castellate, with 2 small setae near the uncinus; segment 2 of peraeopods 3 and 4 not anteriorly lobate; peraeopod 5 nearly as long as peraeopod 7; segment 2 of peraeopods 5-7 expanded and subrectangular, posteroventrally lobate; segment 5 of peraeopods 5-7 shorter than segment 6. Pleopods ordinary; pleopod 2 of male often gonopodous. Posteroventral corner of epimeron 2 not acutely produced; epimeron 3 with a variable number of posterior notches, the posteroventral corner unproduced or with a small tooth.

Peduncles of uropods 1 and 2 not dorsally broadened; rami of uropod 1 subequal; outer ramus of uropod 2 usually shorter than the inner ramus. Uropod 3 extending beyond uropod 1; peduncle without a large process; rami usually equal in length, narrow, lanceolate, and usually with plumose setae.

Lobes of the telson usually fused for less than half its length, each apex usually with 2 or more setae or spines.

Long coxal gills present on peraeopods 2-6 and often with a gill on peraeopod 7 (although this may be reduced or absent in one or both sexes). Sternal gills absent. Female with large oostegites on peraeopods 2-4 and a smaller straplike oostegite on peraeopod 5; oostegite of peraeopod 2 not proximally broadened, not wider than this coxa.

Relationships. "Paramoera" differs from *Paramoerella* Ruffo, 1974, by the larger eye, the cleft inferior antennal sinus, the absence of inner lobes on the lower lip, and the more fully developed gills. It differs from *Sternomoera* Barnard & Karaman, 1982, by the absence of sternal gills; and from *Pseudomoera* Schellenberg, 1929, by the more typical (non-geniculate) segment 5 of the gnathopods. "*Paramoera*" differs from *Moanamoera*, n. s-g., by the larger (pigmented) eye, the cleft inferior antennal sinus, the longer segment 3 of the mandibular palp, the shorter anterior coxae, the stouter gnathopods, the more rectangular segment 2 of peraeopods 5-7, and the less acutely produced epimeron 2. It differs from *Rhithromoera*, n. s-g., by the larger eye, the cleft antennal sinus, the greater setosity of the antennae and maxillae, the shorter segment 1 of the maxillipedal palp, and

the shorter segment 5 of peraeopods 5-7. It is also distinct from *Humilomoera*, n. s-g., in the larger eye, the cleft inferior antennal sinus, the greater setosity of the antennae and maxillae, and the more fully developed gills.
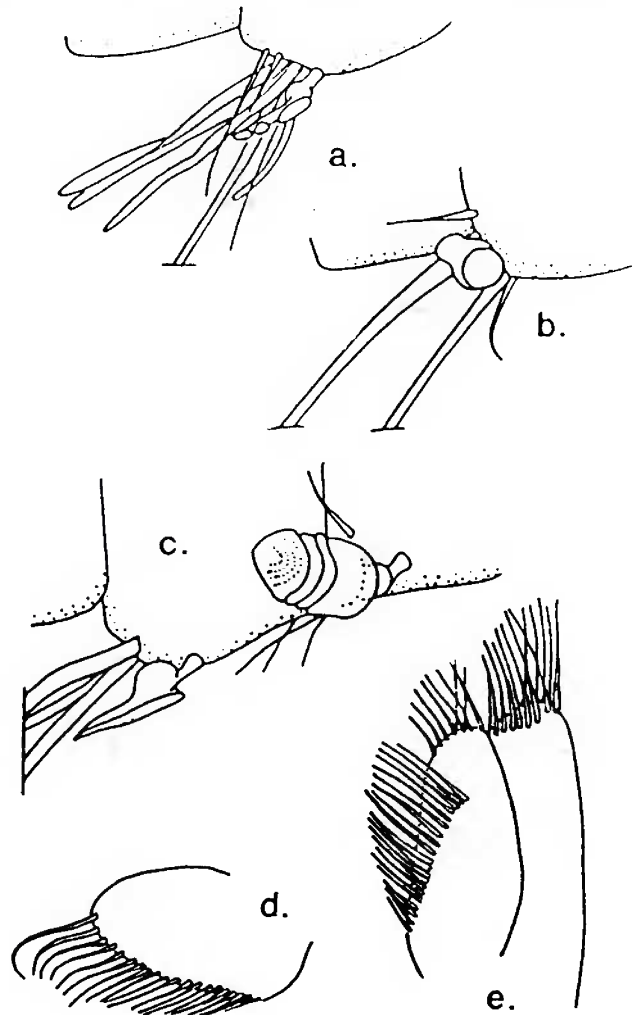

FIG. 1. Calceoli and maxillae of *Paramoera bidentata*, South Africa (SAM 1294 and SAM A12765). a. ventral setal group of a flagellar segment of antenna 1 of the female (with 3-element calceolus); b. ventral setal group of a flagellar segment of antenna 2 of the female (with key-hole shaped calceolus); c. ventral and ventromedial setal groups of the flagellum of antenna 1 of the male (with typical discoid calceoli composed of multiple elements); d. inner plate of maxilla 1; e. maxilla 2.

Component species. This grade tentatively includes all species of *Paramoera* which have not been assigned to the genera *Paramoerella*, *Relictomoera*, *Sternomoera*, or *Pseudomoera*, or to the subgenera *Moanamoera*, *Humilomoera*, or *Rhithromoera* (see Bellan-Santini and Ledoyer, 1974, and Barnard & Karaman, 1991, for comprehensive lists of species). The type species, *P. australis* Miers 1875, and its

close relative, *P. austrina* (Bate 1862), are members of this grade, although *P. austrina* apparently lacks plumose setae on uropod 3 (Thurston, pers. comm.).

The species *P. bidentata* K.H. Barnard, 1932, differs by the toothed dorsum, the more densely setose maxillae and the presence of calceoli in the female (material examined: SAM 1294 *type* and SAM A12765; Fig. 1). These primitive characters place *P. bidentata* close to the ancestral form of *Paramoera* and may justify its placement in a new ("protomoera") subgenus.

Paramoera walkeri (Stebbing, 1906) differs by the toothed dorsum, the reduced setosity of maxillae 1 and 2, and the fusion of its telson lobes, and may qualify as a separate subgenus. *Paramoera hurleyi* Thurston, 1972, is incongruent by its poorly setose antennae and gnathopods, the short segment 3 of the mandibular palp, and the partly fused telson. *Paramoera bousfieldi* n.sp. exhibits intermediate and advanced characters such as a faint cleft in the inferior antennal sinus, somewhat reduced setosity of maxillae 1 and 2, slender gnathopods, and a non-plumose uropod 3; linking this grade to the new apomorphic subgenera *Moanamoera*, *Humilomoera*, and *Rhithromoera*. *Paramoera capensis* (Dana, 1853) is rejected from this grade, and possibly from the entire genus *Paramoera*, on the basis of the unusual setal tufts and the absence of calceoli from the antennae of both sexes, the extreme setosity of the maxillae, the absence of medial setae on segment 6 of the gnathopods, and the foliaceous rami of uropod 3 with serrate margins (material examined: SAM 12181, SAM A3387).

This loose complex of species encompasses a wide range of habitats, usually marine, interstitial in coarse sediment or epiphytic; sub-Antarctic and holo-Pacific.

FIG. 2. *Paramoera mohri*, holotype female, 6.0 mm; Hazard Canyon Reef, California,   a. head and antennal peduncles,   b. urosome with detail of plumose seta.

Paramoera mohri J. L. Barnard
(Fig. 2)

Paramoera mohri J. L. Barnard, 1952: 16-19, pls. 3, 4:-- Barnard, 1975: 348 and 362 (in part).
not *Paramoera mohri* J. L. Barnard, 1969b: 110, fig. 15:-- Barnard, 1975: 348 and 362 (in part), pl.73, fig. 38.

Material examined.

WASHINGTON: Deadman Bay, San Juan Island (48°30.7'N, 123°8.7'W), Staude Station A, quarterly samples of CFN and numerous samples of CPS from May 1976 to March 1986, mid- to low intertidal, gravel beach (>1000 specimens); North Beach (488.6'N,122 47'W), April 1977, collected by CFN and AR from mid-intertidal beach of cobble over coarse sand (1 specimen); Ebey's Landing, Whidbey Island (48°11.5'N, 122°42.5'W), 26 October 1984, collected by CPS and SJS from mid- to high intertidal sandy gravel beach (2 specimens).

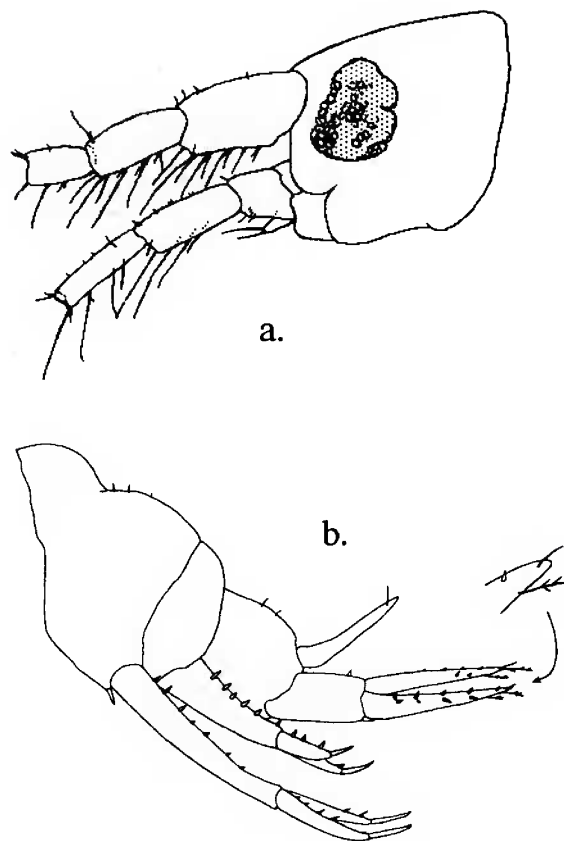CALIFORNIA: Bodega Head (38°18'N, 123°3.5'W), October 1962, collected by G and S from a depth of 10 m in Horseshoe Cove (4 of >100 specimens); Bodega Head (38°18'N, 123°3.5'W), 19 June 1982, collected by CPS from intertidal pocket of coarse gravel between uplifted rock strata (2 of >100 specimens); Carmel Point (36°32'N, 121°56'W), 18 June 1982, Staude Site 1, collected by CPS from an intertidal pool in coarse sand at at the base of cobbles (1 specimen); Hazard Canyon Reef (35°17.2'N, 120°52.8'W), 2 February 1950, collected by JLM and RJM in gravel (holotype and paratypes), AHF #504; Hazard Canyon Reef, 18 September 1987, collected by CPS in gravel (12 specimens); Montana de Oro (35°15.4'N, 120°53.5'W), 1972, collected by JDC and JLC from an intertidal cave pool (3 of >100 specimens), CAS #010535.

Diagnosis. Inferior antennal sinus with a distinct cleft, postantennal lobe extended anteriorly; eye large, dark, oval (its anteroventral corner extended slightly foward); antenna 1 about 10% longer than antenna 2; major peduncular segments of antennae with about 4 groups of long setae along the ventral margins; gland cone usually with 1 long and 1 shorter seta.

Inner plate of maxilla 1 with 5-7 plumose setae; inner plate of maxilla 2 with about 5 plumose setae.

Segment 6 of gnathopod 1 with about 5 posterior groups

of comb setae; segment 6 of gnathopod 2 with 7-8 posterior groups of comb setae; gnathopod 2 of female with segment 5 about 10% longer than segment 6; gnathopod 2 of male with segment 5 about 65% as long as segment 6, segment 6 distally broadened, its palm oblique, palm about 55% as long as the posterior margin.

Posterior margin of segment 6 of peraeopod 4 with about 4 ornamental groups, each consisting of a single barb spine and a lateral seta (distalmost seta accompanied by long setae); posterior margin of segment 2 of peraeopod 7 with shallow notches, segment 4 about 40% as wide as segment 2, longest spines of segment 5 about 75% as long as dactyl, longest spines of segment 6 about 40% as long as the dactyl.

Posterior margin of epimeron 3 with about 3 shallow notches, posteroventral notch enlarged as a small tooth; rami of uropod 1 equal in length (subapical spine of inner ramus not much larger than proximal spines); outer ramus of uropod 2 shorter than inner ramus; urosomite 3 with a slight dorsal boss; rami of uropod 3 with plumose setae; each apex of telson with a stout simple seta and a plumose seta.

Clarification of the holotype. It was earlier reported (Staude, 1986) that the holotype of *Paramoera mohri* (#AHF 504) seemed erroneous, and was possibly mislabeled by Barnard (1969b) when he refigured the species. This can now be confirmed. The true holotype and paratypic specimens of *P. mohri* were found in the open collection of the Los Angeles County Museum (heir to the benthic material of the Allan Hancock Foundation). Although Barnard's (1952) original drawings are reliable, the head and urosome of the holotype are refigured here to further clarify their structure (Fig. 2). The second maxilla, which was not included in the original description, is missing from the holotype.

Barnard's juvenile Carmel specimens of *Paramoera mohri* (J. L. Barnard, 1969b, Fig. 15), as well as some specimens that I collected from Carmel Point, are *Paramoera suchaneki* , new species (p.   ), the only known species in which the inner rami of uropods 1 and 2 are shorter than the outer rami. True specimens of *P. mohri* of the small size (3-4 mm), collected in the present study from Carmel and from Washington, have a more prominent tooth on epimeron 3, uropod 2 with shortened outer ramus, an equiramous third uropod, and shorter telson setae.

Size range. Female to 6.5 mm, male to 5.7 mm.

Color in life. Body nearly colorless, eye dark maroon.

Distribution. Known from northern Washington (48°30'N) to central California (35°N).

Ecology. *Paramoera mohri* lives interstitially in coarse gravel and small cobble. It is primarily intertidal, migrating up and down the beach with the rise and fall of the tide, and occurs nocturnally in the nearshore plankton. Barnard (1952, 1969b, and 1975) erroneously categorized this species as an inhabitant of the rocky intertidal shore, "nestling in algae or surfgrass." The original label of the type specimens shows that they were collected in the gravel adjacent to Hazard Canyon Reef, California.

In coastal gravel beaches *P. mohri* is sometimes found near the water's edge in concentrated densities exceding 100,000/m², and may co-occur with lesser numbers of *P. columbiana*, *P. serrata*, *P. suchaneki*, and *Accedomoera vagor*.

The long setae of the antennae facilitate suspension feeding. *P. mohri* also feeds opportunistically on algal fragments, filamentous diatoms, and detrital deposits, and has been observed to prey on harpacticoid copepods. Ovigerous females are found throughout the year, with an average brood size of 13, but the major recruitment of juveniles occurs in the spring in Washington populations. The biology of this species has been examined in depth (Staude, 1986).

The seasonal range of water temperature at Washington collecting sites is 7-12°C (maximum recorded temperature at California sites was 17°C). This species prefers higher salinities (29-34 ppt).

Remarks. Some of the characters of the diagnosis are based largely on the Washington material (e.g., maxilla 2, oostegites, calceoli, and male gnathopods), all in close agreement with the original description and figures.

Numerous immature specimens collected subtidally from Bodega Head in 1962 are in general agreement with the diagnosis, but have slightly lighter eyes, a difference that might be an artifact of preservation. This is the only known subtidal population of *P. mohri*.

Paramoera mohri lacks a clearly distinctive identifying character. The long setae of its antennae and the plumose setae of the third uropod make it difficult to distinguish from *P. serrata* and juveniles of *P. suchaneki* and *P. columbiana*. Nevertheless, *Paramoera mohri* differs from *P. serrata* by the less developed postantennal lobe, the shallower posterior notches of the hind basal segments, the shorter spines of peraeopod 7, and the less pronounced boss of the urosome. It may be separated from immature *P. suchaneki* and *P. columbiana* by the absence of small barb spines from segment 3 of antenna 2, the shorter subapical spine of the inner ramus of uropod 1, and the absence of colored banding in life. The additional characters of the gland cone, gnathopods, peraeopod 4, telson, and body size are also useful when separating adults of these species.

Paramoera serrata, new species
(Figs. 3A, 3B)

Paramoera serrata Staude, 1986: 46-62, fig. 1.6, fig. 1.7 (in part).
"*Paramoera serrata* Staude (in press)" of Staude, 1987: 376 and 378.

Material examined. Morse Creek, Washington (48°07.1'N, 123°20.7'W), NOAA Station MC+622, 27 July 1976, collected by CFN and AR from high intertidal beach (sandy gravel over buried cobble) east of stream mouth.

Holotype: female, USNM-231313; allotype, male, USNM-231314; 60 paratypes, USNM-231315; 54 paratypes, NMC-IZ1986-055.

Additional material.

WASHINGTON: Morse Creek (48°07.1'N, 123°20.7'W), NOAA Station MC+616, 17 May 1976, collected by CFN and AR from high intertidal beach (sandy gravel over buried cobble) east of stream mouth (11 specimens); Dungeness Spit (48°08.8'N, 123°11.2'W), NOAA sample number OK76302/1#5, from guts of juvenile salmon (*O. kisutch*) in beach seine collection of CS and BM (48 and 61 specimens); Dungeness Spit, NOAA Stations DS+0 and DS+3, spring 1977-winter 1978, collected by CFN and AR from low intertidal sandy-gravel beach (162 specimens); Dungeness Spit, 26 October 1984, collected by CPS and SJS in night plankton tow over low intertidal sand beach (20 specimens). CALIFORNIA: Hazard Canyon Reef (35°17.2'N, 120°52.8'W), 16 June 1982, collected by CPS from mid-intertidal fine gravel beach immediately south of reef (2 specimens); Montana de Oro Beach (35°15.4'N, 120°53.5'W), 16 June 1982, collected by CPS from mid-intertidal coarse sand beach immediately south of stack rock (5 specimens); Ebey's Landing, Whidbey Island (48°11.5'N, 122°42.5'W), 26 October 1984, collected by CPS and SJS from mid-intertidal sandy gravel beach (2 specimens).

Diagnosis.

Eye moderate and dark, ovate; postantennal lobe very large, separated from the lateral lobe by a deep cleft; antenna 1 and 2 nearly equal in length; major peduncular segments of antennae with 5 or more groups of long setae along the ventral margins; gland cone with 4-6 long setae.

Inner plate of maxilla 1 with 5-7 plumose setae; inner plate of maxilla 2 with 4 plumose setae in the diagonal row

Segment 6 of gnathopod 1 with 5-6 posterior groups of comb setae; segment 6 of gnathopod 2 with 6-10 posterior groups of comb setae; in female segment 5 of gnathopod 2 about 70% as long as segment 6; in male segment 5 of gnathopod 2 about 45% as long as segment 6, palm of gnathopod 2 very oblique, palm about 75% as long as the posterior margin.

Posterior margin of segment 6 of peraeopod 4 with 3 ornamental groups, each consisting of a single barb spine and a curved seta on its lateral side (the distalmost spine enlarged and accompanied by additional long setae); posterior margin of segment 2 of peraeopod 7 serrated, segment 4 nearly 50% as wide as segment 2, segments 5-6 with long spines (some as long as the dactyl).

Posterior margin of epimeron 3 with 2 distinct notches, the notch at the posteroventral corner bounded by a small recurved tooth; peduncle of uropod 1 with 7-10 lateral spines; urosomite 3 with a dorsal boss; inner ramus of uropod 3 with plumose setae along the entire inner margin and at the tip of the outer margin, outer ramus with plumose setae along the distal half of the inner margin; each apex of telson usually with 1 slender spine and a plumose seta (occasionally 1-2 stout barb spines at each apex).

Coxal gill of peraeopod 7 small, present only in female.

Size range. Female to 6.0 mm, male to 4.6 mm.

Color in life. Body and all appendages translucent white with very faint pink banding along the sutures of peraeonites, eye red.

Distribution. Known from the Washington shore of the Strait of Juan de Fuca (latitude 48°N) to central California (35°N), with a distinctive southern subspecies found in Baja California (32°N).

Ecology. *Paramoera serrata* is a shallow burrower in coarse sand and gravel sediments of wave exposed beaches. The widened posterior peraeopods with enlarged spines may be an adaption to this burrowing habit (e.g., similar to some species of the Haustoriidae). The well-developed, regularly spaced setae of the antennae and gnathopods are probably used in suspension feeding. The nocturnal presence of this species in the plankton is similar to the behavior of *P. mohri*. Brood size is about 12 ova. Recorded water temperatures at the collecting sites range from 6.3°C (winter) to 11.2°C (summer), with a mean salinity of 29.4 ppt (Nyblade, 1979).

Remarks. *Paramoera serrata* exhibits several derived characters, and seems to occupy a niche that is somewhat removed (although not exclusive) from its congeners. The expanded postantennal lobe of the head, the subequal length of the antennae, the extremely setose maxillipedal palp, the enlarged distal spine of pereopods 3 and 4, the long spines of peraeopods 5-7, and the boss of urosomite 3 are unique. The serration of segment 2 of peraeopods 5-7, and the sculpture of epimeron 3 are distinctive characters similar to those of the new subgenus *Humilomoera*. The exceptionally setose antennae and gland cone suggest an affinity to *Paramoera suchaneki*, new species (See "Remarks" under *P. mohri* for identification of juveniles).

Etymology. The species name refers to the serrated posterior margins of the basal segments of peraeopods 5-7.

Paramoera serrata escofetae, new subspecies
(Fig. 4)

Paramoera serrata Staude, 1986 (in part): 49, 59-62.

Material examined.

BAJA CALIFORNIA: Grenada Cove, Ensenada, Mexico (31°53'N, 116°41'W), 1 March 1980, collected by AE from low intertidal cobble beach (32 specimens).
Holotype: female (LACM #94-41-1), allotype, male (LACM #94-41.2); 30 paratypes (LACM #94-41.3 and CPS).

Diagnosis. This subspecies if closely similar to the northern form of *P. serrata* in having subequal antennae with long filtering setae, a deep cleft of the inferior antennal sinus,
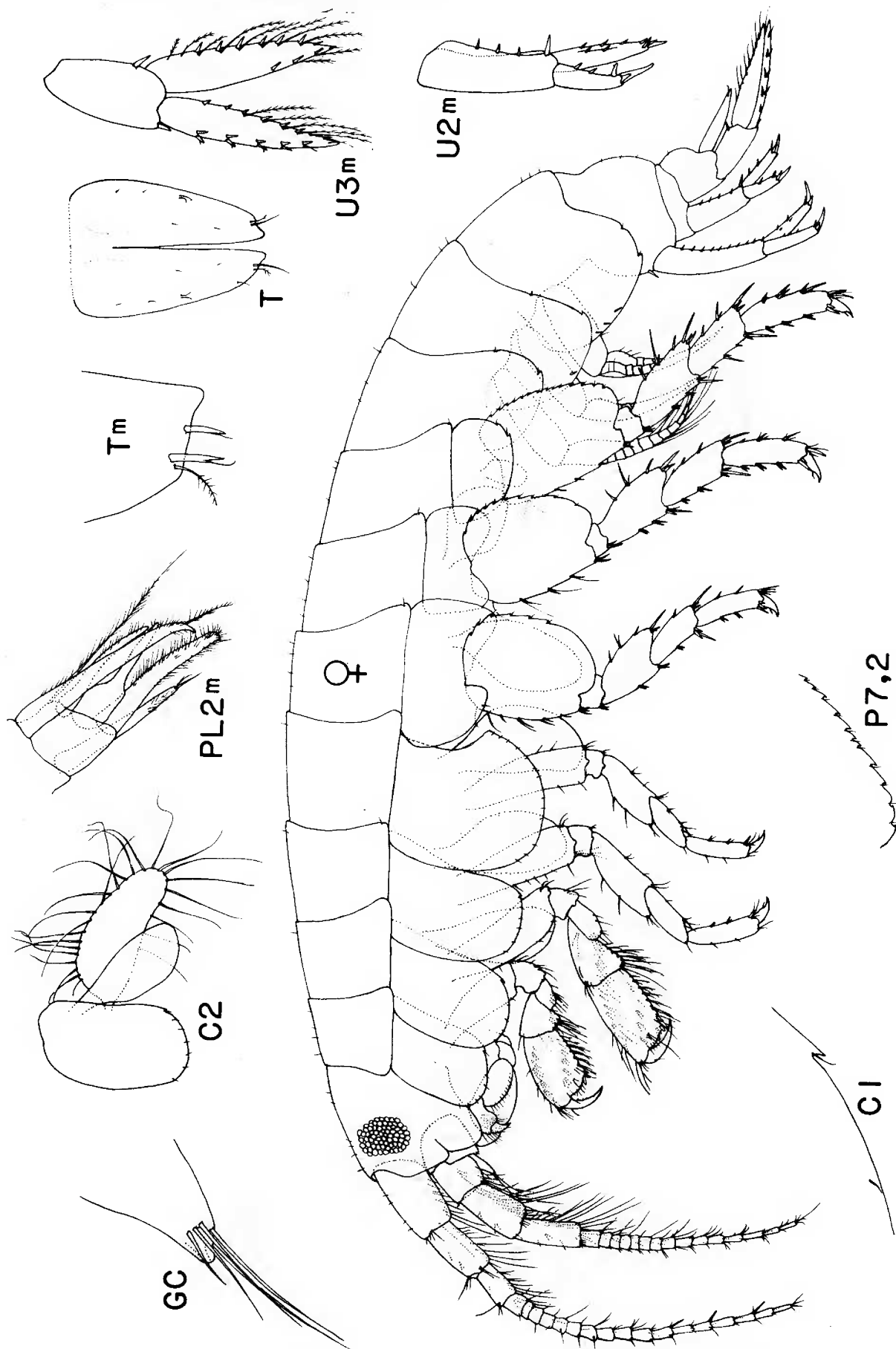
FIG. 3A. *Paramoera serrata,* new species. Holotype female (4.3 mm). m = allotype male (4.0 mm). Morse creek, WA.
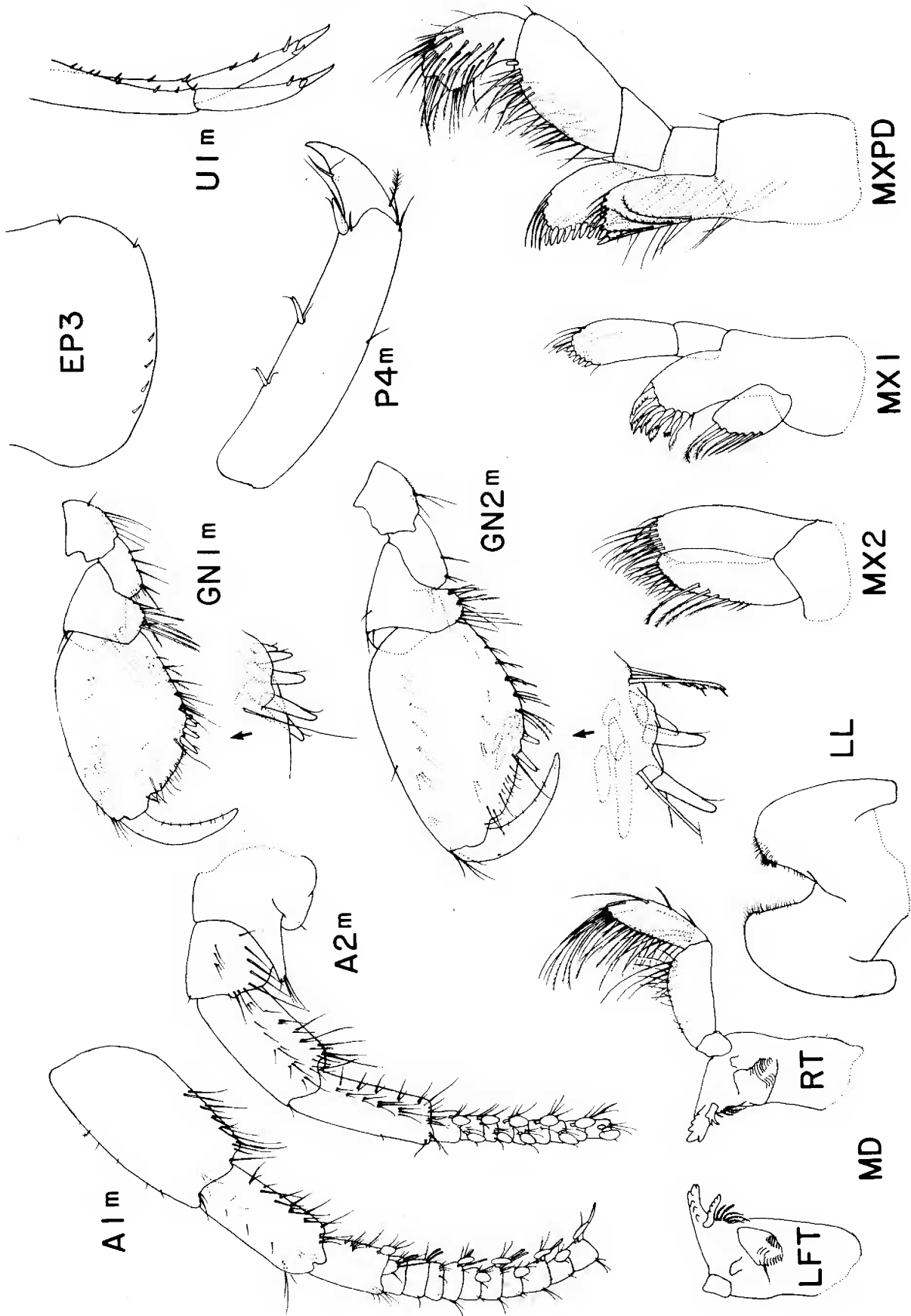
FIG. 3B. *Paramoera serrata,* new species. Holotype female (4.3 mm). m = allotype male (4.0 mm). Morse creek, WA.

similar mouth parts, a very setose gland cone and gnathopods, similar ornamentation of the epimera, and a single slender spine on each apex of the telson. They are distinct from northern *P. serrata* by the more spinose segment 6 of peraeopod 4, the less serrated posterior margins of segment 2 of peraeopods 5-7, the shorter distal spines of segments 4-5 of peraeopod 7, and the less pronounced boss of urosomite 1. The eye is unpigmented (perhaps an artifact of preservation).

Size range. Female to 7.0 mm, male to 6.0 mm

Color in life. Unknown

Distribution. Known only from the type locality, Baja California (latitude 32°N).

Ecology. The type locality is a beach of clean cobbles and sand that is seasonally resorted by wave action. This habitat is unusual for the northern *P. serrata*, which prefers coarse sand and gravel. The Ensenada population may instead be concentrated in a shallow subtidal sand berm, which is adjacent to these intertidal cobbles (pers. obs. of 12 June 1982). Females collected in March were ovigerous, with about 12 eggs.

Remarks. Specimes collected at Ensenada, Mexico, are recognized here as a southern subspecies of *P. serrata*, but possibly constitute a separate species. Its status may be resolved by future collections and studies of its behavioral ecology, in contrast to the northern form.

Etymology. This subspecies is named in honor of Ms. Anamaria Escofet, professor of biology at Centro de Invest. Cientificas, in Ensenada, Baja California, Mexico, who collected these specimens. Professor Escofet has also contributed to our knowledge of the amphipod fauna of Argentina.

FIG. 4. *Paramoera serrata escofetae* n. s-sp. female holotype (6.5 mm), Ensenada, Mexico. (A2 in medial view).

Paramoera suchaneki , new species
(Figs. 5A, 5B)

Paramoera mohri J. L. Barnard, 1969b: 110-111, fig. 15.--Barnard, 1975: 348 and 362 (in part), pl. 73, fig. 38.
Paramoera cf. *mohri* Suchanek, 1979: 136, Appendix VI.
Paramoera suchaneki Staude, 1986: 63-82, figs. 1.8 and 1.9.
"*Paramoera suchaneki* Staude (in press)" of. Staude, 1987: 376 and 378.

Material examined.
Tatoosh Island, Washington (48°24'N, 124°44'W), Suchanek Station T/5L, May and July 1976, collected by THS in mussel bed (*M. californianus*), low intertidal, wave-exposed, rocky beach.
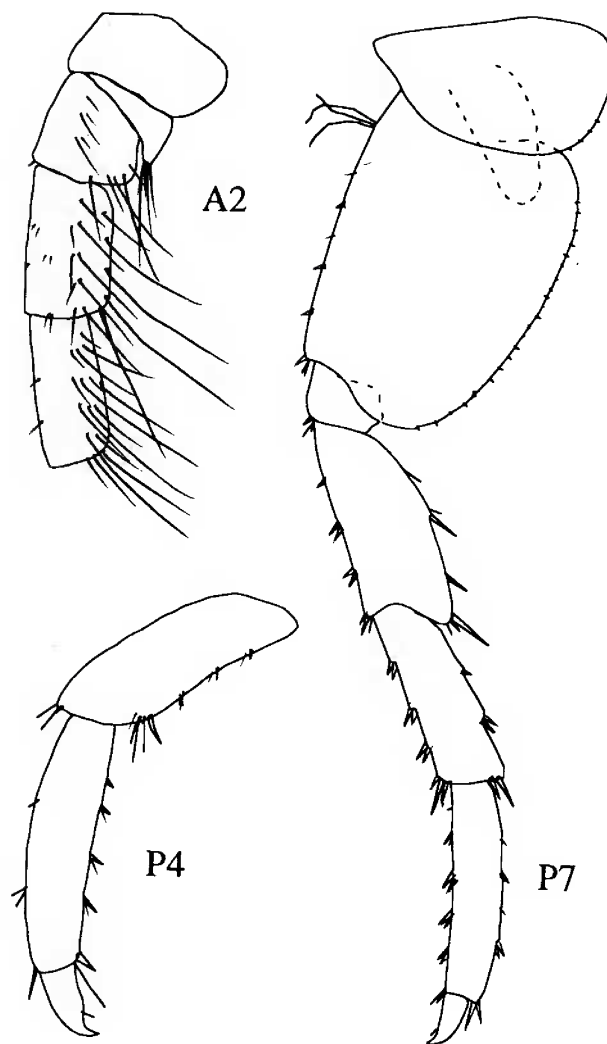**Holotype**: female, USNM-231316; allotype, male, USNM-231317; 8 paratypes, USNM-231318; 2 paratypes, NMC-IZ1986-055.

Additional material.
ALASKA: Hogan Island, S.E. Alaska (57°43'N, 136° 15'30"W), NMC Station S5B10, 28 July 1980, collected by ELB under open stones, mid-intertidal (1 female); Dry Pass, Hill Island, Chichagof Island (57°47'N, 136°18'W), NMC Station S7B6, 29 July 1980, collected by ELB under bare stones, mid- to high intertidal (1 immature female); Trap Point, Slocum Arm, Chichagof Island (57°33.5'N, 136°01'W), NMC Station S3B2, July 1980, collected by ELB beneath kelp zone, low to mid-intertidal (1 immature female); Column Point, Lisianski Strait (58°06.5'N, 136°27'W), NMC Station S11B4-5, July 1980, collected by ELB intertidally under open boulders (1 ovigerous female, 1 male).
BRITISH COLUMBIA: Nesto Point, Graham Island (53°27'N, 132°48'W), NMC Station W4a, 11 August 1957, collected by ELB among shell fragments and boulders, low intertidal (3 specimens).
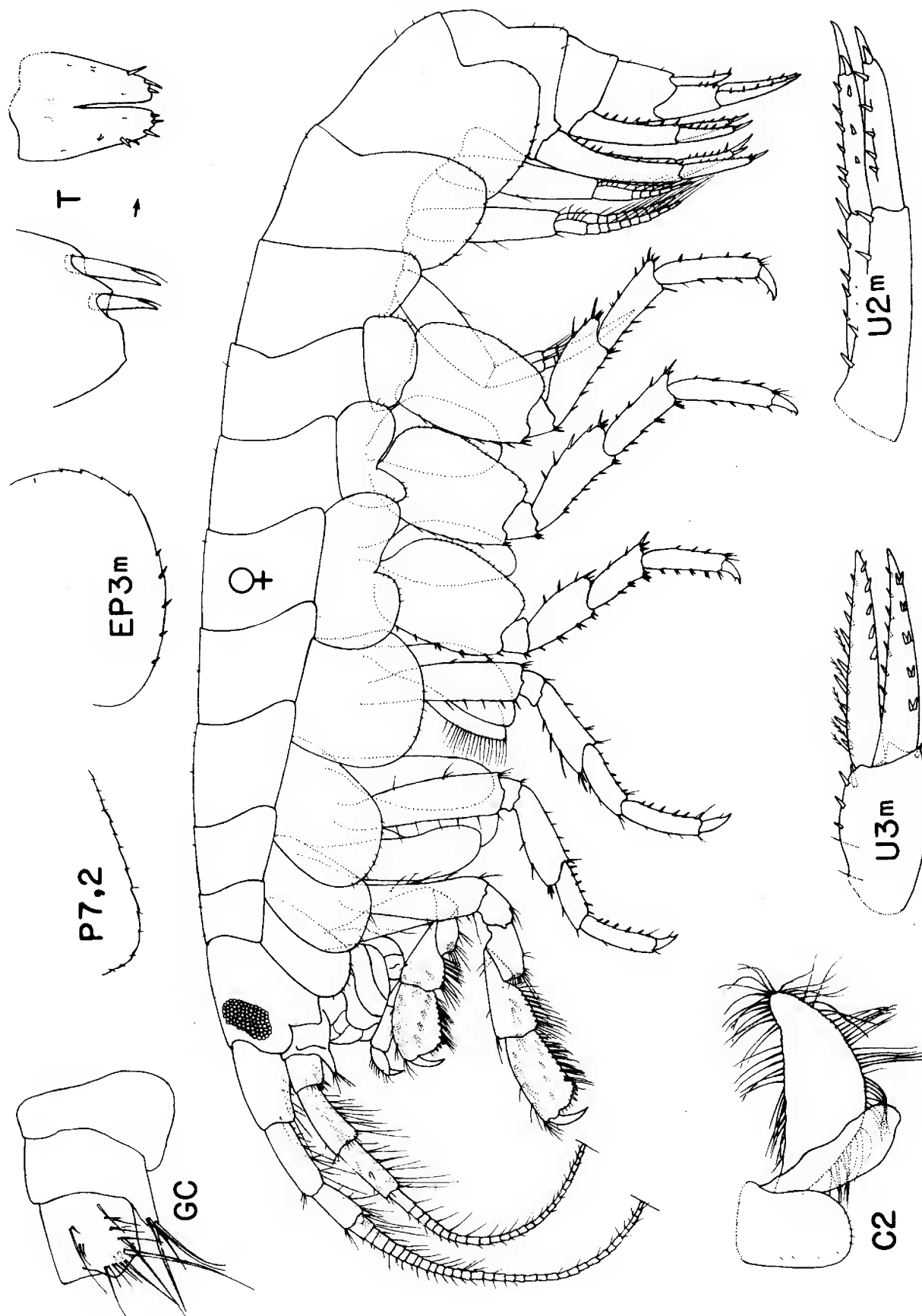
FIG. 5A. *Paramoera suchaneki*, n. sp. holotype female (12.0 mm); m = allotype male (8.0 mm). Tatoosh I., WA.
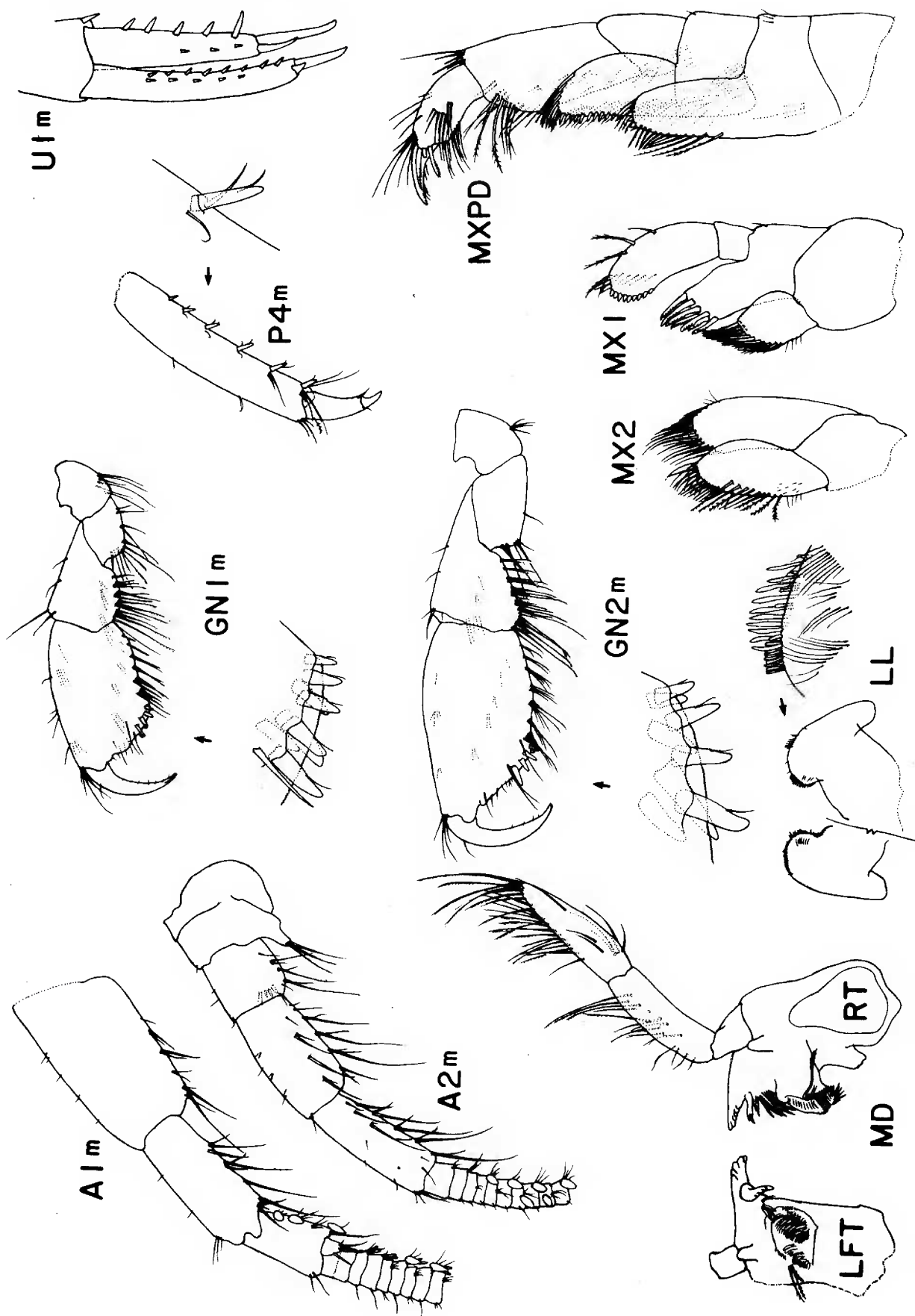
FIG. 5B. *Paramoera suchaneki*, n. sp. holotype female (12.0 mm); m = allotype male (8.0 mm). Tatoosh I., WA.

WASHINGTON: Tatoosh Island (48°24'N, 124°44'W), Suchanek Stations T/2, T/4, and T/5, July 1974, April and September 1975, May and July 1976, replicate samples collected by THS in mussel bed (*M. californianus*), low to mid-intertidal, wave-exposed, rocky beach (>200 specimens); Shi-Shi Beach (48°17'N, 124°41'W), Suchanek Station S/1, July 1974, April and September 1975, May and July 1976, replicate samples collected by THS in mussel bed (*M. californianus*), mid-intertidal, rocky bench (>100 specimens); Goose Island (48°27.5'N, 122°57.3'W), 16 April 1983, collected by CPS under cobbles on gravel and sand, mid- to high intertidal (25 specimens); Deadman Bay, San Juan Island (48°30.7'N, 123°08.7'W), Staude Station C, 15 July 1983 and monthly samples January-December 1984, collected by CPS under cobbles and among boulders on sand and gravel, mid-intertidal (>100 specimens).
CALIFORNIA: Carmel Point (36°32'N, 121°56'W), Barnard Station 48-X-1, 30 December 1963, collected by JLB intertidally from unknown substratum (4 of 7 specimens; AHF collection); Carmel Point (36°32'N, 121°56'W), Staude Site 4, 18 June 1982, collected by CPS from intertidal pockets of gravel among rocks (4 specimens).

Diagnosis. Eye large and dark, slightly reniform; inferior antennal sinus with a small cleft; antenna 1 about 10% longer than antenna 2; peduncles of antennae with 4-6 groups of long setae along the ventral margins of each segment; gland cone with about 5 long setae; inner plate of maxilla 1 with 9-11 plumose setae along the inner margin; inner plate of maxilla 2 with 6-9 plumose setae in the diagonal row; segment 6 of gnathopod 1 with 6-8 groups of comb setae along its posterior margin; segment 6 of gnathopod 2 with 7-10 groups of comb setae along its posterior margin; in male segment 5 of gnathopod 2 about 80% as long as segment 6, palm of gnathopod 2 oblique, palm about 60% as long as posterior margin of segment 6; in female segment 5 of gnathopod 2 greater than or equal in length to segment 6, palm of gnathopod 2 nearly transverse, palm about 30% as long as the posterior margin of segment 6; posterior margin of segment 6 of peraeopod 4 with a row of about 6 ornamental groups, each consisting of a single barb spine with a small curved seta on either side; posterior margin of segment 2 of peraeopod 7 minutely serrated, segment 4 about 40% as wide as segment 2, largest spines of segments 5 and 6 less than 33% as long as the dactyl; posterior margin of epimeron 3 minutely serrated, with a small seta emerging from each of 5 or 6 slight notches; posteroventral corner of epimeron 3 not strongly developed; uropod 3 with plumose setae proximally along the inner margin of the inner ramus and often with a few plumose setae proximally along the inner margin of the outer ramus; each lobe of the telson with 2-3 short apical spines and a longer proximal spine; gills epecially long, but lacking a gill on peraeopod 7 in both sexes.

Size range. Female to 13 mm; male to 10 mm.

Color in life. Antennae with red-brown tint; eye nearly black; peraeonites with dorsal pigment patches which form a symmetrical mottled pattern about the sagittal midline, these patches either brown or olive. Pleon of some Alaskan specimens with a pink tint. Juveniles with purple banding at sutures of peraeonites.

Distribution. Known from Southeast Alaska (latitude 58°N) to northern California (latitude 36°30'N).

Ecology. *Paramoera suchaneki* is a nestler at the base of boulders and rocks on gravel/sand in the mid intertidal zone with moderate to strong wave exposure. It is occasionally abundant interstitially among the byssal threads, shells, and associated detritus of dense mussel beds (*Mytilus californianus*). Its setose antennae and gnathopods are presumed to assist it in the collection of suspended chain-forming diatoms and algal fragments as well as settled detritus. Washington populations occur at salinities of 28-32 ppt, and temperatures of 8-15°C.

Remarks. With maturity, the eye becomes more reniform, antennae and gnathopods become more setose, and peraeopods become more spinose. Hence, juveniles are easily confused with other species, but may be distinguished by the shorter inner ramus of uropods 1 and 2.

This species was mistaken for *Paramoera mohri* by J. L. Barnard (1969b; his Fig. 15), and is lumped with *P. mohri* in his later work (J. L. Barnard, 1975).

There is a surprising degree of similarity between *Paramoera suchaneki* and *P. austrina* (Bate, 1862) of the southern hemisphere. Comparison to a redescription (M. H. Thurston, unpub.) of Bate's type specimens indicates that the head, antennae, gland cone, mouthparts, gnathopods, peraeopods, epimera, uropods, and telson are in fairly close agreement, except as follows: *P. austrina* with setae of antennae shorter and less abundant, maxilla 2 with diagonal setal row extending 50% across the face of the inner plate, dactyls of gnathopods with minutely serrate inner margin, segment 6 of peraeopod 4 apparently with 2-3 spines in each spine group of the posterior margin (although segment 6 of peraeopod 3 seems to have only single spines), uropod 1 with 27 spines along the lateral margin of the peduncle and 14 spines along the lateral margin of the outer ramus, uropod 2 outer ramus slightly shorter than the inner ramus, uropod 3 apparently without plumose setae, each lobe of telson with an additional proximal spine near the lateral margin (about 60% back from the apex).

Similarities are also recognized between *P. suchaneki* and *P. koreana* Stephensen 1944. The antennae, gnathopods, peraeopods, and uropod 3 are in close agreement in these species. However, *P. koreana* is distinguished by the single seta on the gland cone, the reduced setosity of the maxillae, the distinct tooth at the posteroventral corner of epimeron 3, the greater spinosity of uropod 1 (while lacking the enlarged distal spine of the peduncle), the single seta on each lobe of the telson, and the smaller size at maturity (5 mm).

Paramoera brevirostrata (Bulytscheva, 1952), originally

recognized as *Pontogeneia* and more recently placed in *Accedomoera* (Thurston, 1972), also exhibits similarity to *P. suchaneki* in the eye, antennae, gland cone, and gnathopods. Comparison to Bulyscheva's original illustrations (which are lacking in detail) would suggest that *P. brevirostrata* can be distinguished by the apparent lack of a cleft in the inferior antennal sinus, the fewer setae on the inner plates of maxilla 2 and maxilliped, the more setose margins of coxae 1 and 2, the lack of plumose setae on uropod 3, and the shape and ornamentation of the telson (each acutely tapered lobe with a single seta). It should be noted that in 1972 Barnard suggested that *P. brevirostrata* was a "probable synonym" of *P. japonica* (Tattersall, 1922). More recently, however, Barnard & Karaman (1982) have transferred *japonica* to the genus *Sternomoera*. The setose nature of the telson, the sternal gills, and the freshwater habitus of *S. japonica* are quite distinctive, and warrant continued separation of these species.

Etymology. Named in honor of Dr. Thomas H. Suchanek, who originally discovered this species in his studies of the *Mytilus californianus* community. This and other research performed on Tatoosh Island under the supervision of Dr. Robert T. Paine have greatly increased our knowledge of the ecology of rocky shores.

Paramoera columbiana Bousfield

Paramoera columbiana Bousfield, 1958: 62-64, figs. 1, 2.-- Bousfield & Hubbard, 1968: 2-3.-- Staude, 1986: 83-88, fig. 1.10.--Staude, 1987: 376 and 378.

Material examined.
ALASKA: Amchitka Island (51°28'N, 179°07'E), O'Clair Station IA-2, plot 9, 23 October 1972, collected by CEO on uplifted bedrock reef (1 specimen; NMC 1976-30); St. Paul Island, Pribilof Islands (57°10'N, 170°30'W), 30 November 1979, collected by CEO from high intertidal lagoon (1 specimen); Olsen Bay, Prince William Sound (60°45.5'N, 146°11'W), NMC Station SB2, August 1965, collected by JDH at the mouth of Olsen Creek (1 specimen); Steamer Bay, Etolin Island (56°8'N, 132°40'W), summer 1981, collected by MLM from cobble sediment in the tidal reach of Porcupine Creek (10 specmens); Port McArthur Bay, Kuiu Island (56°5'N, 134°10'W), NMC Station A15, collected by ELB (1 specimen); Pt. Marsh, Prince of Wales Island (54°43'N, 132°17'W), NMC Station A5, collected by ELB (3 specimens).
BRITISH COLUMBIA: Hay's Creek, Prince Rupert (54°18'N, 130°20'W), NMC Station P3, 3 July 1957, collected by ELB from mouth of creek (2 specimens; ELB slide mount); Kitimat (54°02'N, 128°45'W), 7 October 1981, Station DS441, collected by SC from intertidal beach (4 specimens); Queen Charlotte City (53°16'N, 132°04'W), NMC Station E8, 17 August 1957, collected by ELB from

stones and moss in small stream (>50 specimens); Stiu Point, Graham Island (53°14'N, 132°36'W), NMC Station W6, 29 July 1957, collected by ELB from bedrock pools at stream mouth (11 specimens); Gray Bay, Moresby Island (53°08'N, 131°43'W), NMC Station E21, 12 July 1957, collected by ELB from high intertidal, freshwater pools on a rock and boulder shore (holotype, allotype, and 24 paratypes; NMC 2277); Cape Fanny, Moresby Island (52°07'N, 131°09'W), NMC Station W6, collected by ELB from stream mouth (1 specimen); Dutchman Head, Knight Inlet (51°05'N, 125°35'W), NMC Station N14, 25 June 1959, collected by ELB from intertidal fine silt and fucoids on bedrock (3 of 14 specimens); Simms Creek, Vancouver Island (49°48'N, 125°11'W), NMC Station V21, 28 July 1959, collected by ELB from coarse sand and stones with woody detritus in in brackish water (5 specimens); Porteau Cove, Howe Sound (49°33'N, 123°14.2'W), collected by CL from unknown substratum (14 of 39 specimens); Cowichan River estuary, Vancouver Island (48°46'N, 123°36'W), 9 February 1978, collected by ELB from *Fucus* and leaf litter (8 of 17 specimens); Mount Douglas Beach, Victoria (48°30'N, 123°20.3'W), 20 April 1983, collected by PS from high intertidal (2 specimens); Muir Creek, Vancouver Island (48°22.8'N, 123°52'W), 1 May 1983, collected by PS at mouth of creek (18 specimens).

WASHINGTON: Deadman Bay, San Juan Island (48°30.7'N, 123°8.7'W), Staude Station B, 1 June 1983, collected by CPS on low intertidal gravel beach (2 specimens); Morse Creek (48°07.1'N, 123°20.7'W), NOAA Station MC+004, 17 May 1976, collected by CFN and AR from low intertidal beach (sandy gravel and cobble) east of stream mouth (2 specimens); Carkeek Beach, Seattle (47°42.8'N, 122°22.7'W), METRO Station C7+613, collected by JWA and CPS from mid-intertidal mixed sediment beach near small stream (2 specimens).

Diagnosis. Eye large and dark, reniform; postantennal sinus with a cleft; antenna 1 about 10% longer than antenna 2; segment 1 of antenna 1 with 2-3 short barb spines at the distoventral corner; major peduncular segments with about 3 groups of moderate length setae along the ventral margins (reduced in male), gland cone of female with 1-2 barb spines and 1-2 setae, male with 2-3 barb spines (no setae).
Inner plate of maxilla 1 with 5-6 plumose setae; inner plate of maxilla 2 with 4-5 plumose setae in the diagonal row.
Segment 6 of gnathopod 1 with 3-4 posterior groups of comb setae; segment 6 of gnathopod 2 with 5-6 posterior groups of comb setae and with sparce mesial setae; gnathopod 2 of female with segment 5 about 20% longer than segment 6; gnathopod 2 of male with segment 5 about as long as segment 6, palm very oblique and poorly defined, about as long as the posterior margin.
Posterior margin of segment 6 of peraeopod 4 with about 5 ornamental groups, each consisting of 2-3 barb spines; posterior margin of peraeopod 7 with shallow notches, segment 4 about 40% as wide as segment 2, spines of segments 5 and

6 not longer than 55% of the dactyl.

Posterior margin of epimeron 3 with 2-6 shallow setose notches, posteroventral corner with a minute tooth (without seta); uropod 2 with outer ramus only slightly shorter than the inner ramus; uropod 3 with plumose setae; each apex of telson with 1 barb spine, 1 long stout seta, and a small plumose seta.

Coxal gills small; coxa 7 with gill (both sexes).

Size range. Both sexes to about 9 mm (11 mm in northern populations).

Color in life. Body transluscent with purple banding; eye dark.

Distribution. West to Amchitka Island (179°E), and from the Pribilof Islands (57°N) to central Puget Sound (47°40'N).

Ecology. *Paramoera columbiana* has been widely collected in a variety of habitats (e.g., spray pools, rock benches, and tidal reach of streams). It is apparently euryhaline, but is frequently found in areas of reduced salinity near stream mouths. The presence of both spines and long setae on the antennae suggests an omnivorous diet. Ovigerous females have been found from May to July. Fecundity is high in this species; up to 41 eggs per brood. The absence of modified pleopods in the male further suggests that the reproductive biology of *P. columbiana* is different from that of other local species of the *Paramoera* group.

Remarks. Juveniles are particularly difficult to distinguish from *P. mohri* and *P. suchaneki* because the spinosity of the gland cone, peraeopod 4, and the telson increases with maturity. Immature specimens of *P. columbiana* can be recognized by the presence of barb spines distally on the ventral margin of segment 1 of antenna 1 and the dorsal margin of segment 3 of antenna 2, and by the enlarged subapical spines on the inner rami of uropods 1 and 2.

The number of setose notches along the posterior margin of epimeron 3 is variable (holotype with 6, and male paratype with 4), while specimens from Steamer Bay, Alaska (5 mm immature female), and Seattle, Washington (8 mm brooding female) have as few as 2. In nearly all cases the posteroventral tooth of epimeron 3 is very small and asetose.

This is the only local species of *Paramoera* (sensu lato) known to exhibit sexual dimorphism in the ornamentation of the gland cone. The palm of gnathopod 2 is also sexually modified. It is the only species of this group to lack the gonopodous condition of the second pleopod in the male.

An 11 mm immature female (with early stage oostegites) from the Pribilof Islands was examined. Its characters are in general agreement with the diagnosis (some exceptions being the more setose gnathopods and an additional barb spine on one apex of the telson), but its large size suggests a northern race of *P. columbiana* with a modified life history pattern.

Paramoera bousfieldi , new species
(Figs. 6A, 6B)

"*Paramoera* undescribed species" Armstrong et al., 1976.
"undescribed species near *Paramoera mohri*" Staude et al., 1977.
Paramoera bousfieldi Staude, 1986: 89-103.
"*Paramoera bousfieldi* Staude (in press)" of Staude, 1987: 376-378.

Material examined.
Indian Beach, San Juan Island, Washington (48°27.4'N, 122° 57.7'W), 18 May 1984, collected by CPS under cobbles and in shallow sand deposits over a hard clay bench, mid-high intertidal.
Holotype: female, USNM-231319; allotype, male, USNM-231320; 18 paratypes, USNM-231321; paratypes, NMC-IZ1986-055.

Additional material.
ALASKA: Rakof Island, Dry Pass (56°44.5'N, 135°18.5'W), NMC Station S20B4, 3 August, 1980, collected by ELB under stones in eel grass, low intertidal, stream mouth (1 specimen).
BRITISH COLUMBIA: Nesto Point, Graham Island (53°27'N, 132°48'W), NMC Station W4a, 12 August 1977, collected by ELB from low intertidal shell fragments and boulders over bedrock (2 specimens); Horn Rock, Tasu Sound (52°46'N, 132°03'W), NMC Station W16, 10 August 1957, collected by ELB in high water pools (2 specimens); McNab Creek, Howe Sound (49°33.8'N, 123°22.8'W), 21 March 1973, collected by CL near stream mouth (55 specimens); Sarita River Estuary, Barkley Sound (48°53.2'N, 125°00.5'W), NMC Station B14, 2 July 1976, collected by ELB under stones at stream mouth (2 specimens); Victoria Breakwater (48°24.8'N, 123°23'W), 1976, collected by RJL (1 specimen).
WASHINGTON: Lincoln Park Beach, Seattle (47°31.7'N, 122°23.8'W), July 1974, METRO transect 15, collected by JWA and CPS from high intertidal seepage area in shallow mixed sediment over a clay bench (21 specimens); Tongue Point, Strait of Juan de Fuca (48°10'N, 123°40.2'W), NOAA Station TP+3(04), 1 May 1976, collected by CFN and AR from mid intertidal rocky beach (1 specimen); Tatoosh Island (48°24'N, 124°44'W), Suchanek Station T4H, July 1976, collected by THS in high intertidal mussel community (1 specimen); Long Beach (46°19'N, 124°04'W), NMC Station W45, 3 July 1966, collected by ELB from intertidal surf-pounded sand over bedrock (1 specimen).
OREGON: Tillamook Bay (45°30.5'N, 123°56.5'W), NMC Station W65, 17 August 1966, collected by ELB from intertidal coarse sand over clay and embedded stones, brackish (1 specimen).

Diagnosis. Eye large and dark, ovate; inferior antennal sinus deep, with a shallow cleft; antenna 1 about 25% longer than antenna 2; peduncles of antenna 2 with 2-3 groups of
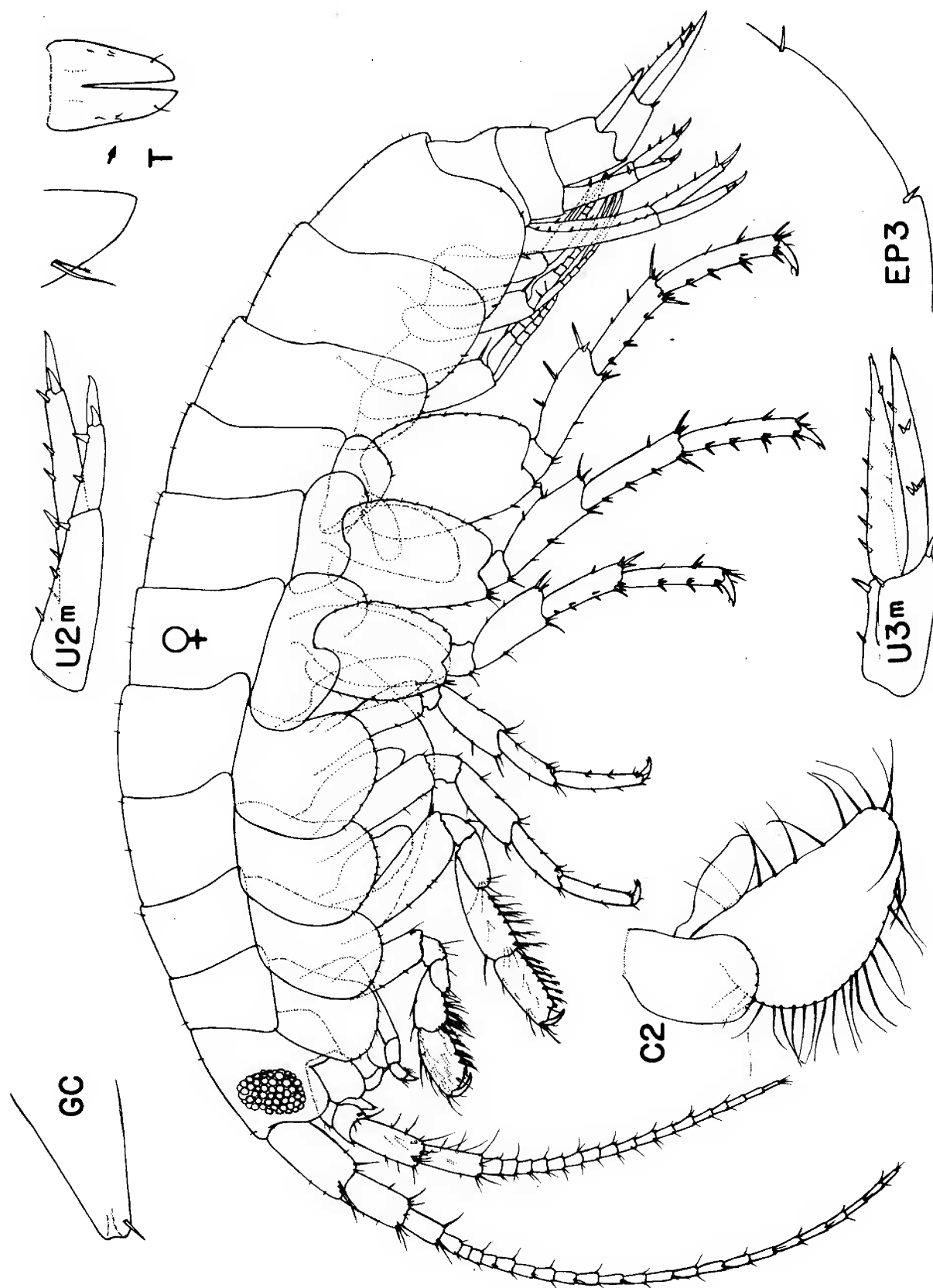
FIG. 6A. *Paramoera bousfieldi*, n. sp. holotype female (4.3 mm); allotype male (3.0 mm). San Juan Island, Washington.
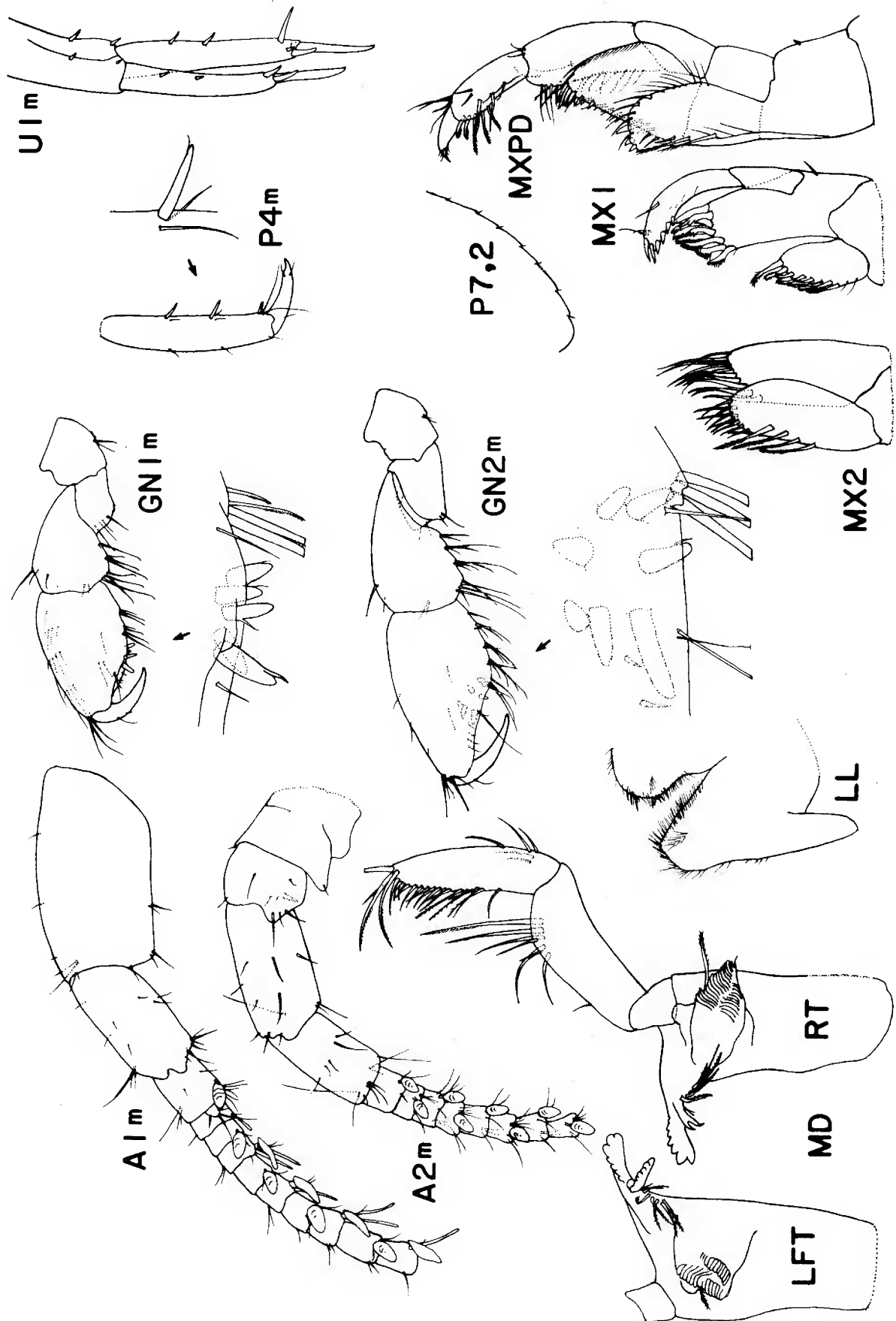
FIG. 6A. *Paramoera bousfieldi*, n. sp. holotype female (4.3 mm); allotype male (3.0 mm). San Juan Island, Washington.

medium-length setae along the ventral magins of each segment; gland cone with a single short seta.

Inner plate of maxilla 1 with 6-7 plumose setae; inner plate of maxilla 2 with 4 plumose setae in the diagonal row.

Segment 6 of gnathopod 1 with 3 groups of comb setae along the posterior margin; segment 6 of gnathopod 2 with 4-6 groups of comb setae along the posterior margin; in male segment 5 of gnathopod 2 about 85% as long as segment 6, palm of gnathopod 2 very oblique, palm nearly equal in length to the posterior margin; in female segment 5 of gnathopod 2 about 135% as long as segment 6, palm of gnathopod 2 about 20% as long as the posterior margin; posterior margin of segment 6 of peraeopod 4 with a row of 3 ornamental groups, each consisting of a slender barb spine and 1-2 setae; posterior margin of peraeopod 7 minutely serrated, segment 4 about 40% as wide as segment 2, largest spines of segments 5 and 6 about 75% as long as the dactyl.

Posterior margin of epimeron 3 with a single notch and seta proximal to a slightly enlarged tooth-like notch and seta at the posteroventral corner; uropod 3 lacking plumose setae; each lobe of telson rather acutely pointed, lacking apical notches or spines, but with a long slender spine subapically near the lateral margin; size to about 4.5 mm.

Size range. Male to 4 mm; female to 4.5 mm.

Color in life. Body translucent white, with light purple banding at articulations of peraeonites and pleonite 1; similar purple blushing on antennae and posterior margins of coxae; eye reddish.

Distribution. Known from southeast Alaska (56°N) to northern Oregon ($45^{\circ}30'$N).

Ecology. Commonly occuring under rocks or in shallow sediment deposits at stream mouths or freshwater seeps where temperature and salinity fluctuate widely over the course of the tidal cycle. Its exact position on the beach is determined more by seepage than tide level. Gnathopods have a full complement of comb setae, but setosity of antennae is reduced, suggesting that surface deposit feeding is of greater importance than suspension feeding in this species. Brood size ranges from 13-19 eggs.

Remarks. *Paramoera bousfieldi* is set apart from the other members of the grade "*Paramoera*" by a number of apomorphic characters. The cleft of the inferior antennal sinus is minute, the antennal setae are reduced, the setosity of the maxillae is intermediate, the brood plates are of the broad form, and the third uropod lacks plumose setae. The palm of gnathopod 2 in the male is very oblique, as in *P. columbiana*. The setosity of the maxillae, the elongate carpus of gnathopod 2 in the female, and the slender distal segments of the posterior peraeopods bear resemblance to characters of the subgenus *Moanamoera*.

Etymology. Named in honor of Dr. E.L. Bousfield, who originally discovered this species in 1957 (unpublished). Through his many years of field collection and museum research, Dr. Bousfield has become the foremost authority on gammaridean amphipods of the eastern North Pacific region.

Paramoera (Moanamoera), new subgenus

Type species. *Paramoera (Moanamoera) rua* J. L. Barnard, 1977.

Diagnosis. Rostrum unproduced; lateral cephalic lobe mammiliform; inferior antennal sinus shallow and without a cleft. Eye reduced or absent, oval, unpigmented. Antennae of moderate length, antenna 1 not much longer than antenna 2; peduncular segments of antenna 1 progressively shorter, segment 1 shorter than head; accessory flagellum 1-segmented, scale-like; ventromedial setae of peduncles short; gland cone with 2-3 moderate setae; calceoli present only in male.

Upper lip entire and subrounded; epistome unproduced. Molar triturative, oval; palp segment 2 longer than 3; lower lip without distinct inner lobes. Maxilla 1: inner plate with 7-10 plumose setae, outer plate with 9-10 pectinate spines; palp long, segment 1 short. Maxilla 2: inner plate not broader nor longer than outer plate, inner plate with a submarginal row of 4-5 plumose setae. Maxilliped: inner plate about as long as outer plate, outer plate with about 8-10 medial spine teeth; palp of 4 segments, segment 1 with a small distolateral extension (but its lateral margin distinctly shorter than that of segment 2), segment 3 with a slight distal lobe, segment 4 shorter than segment 3, segment 4 not spinose (but with small distal setae) along the inferior margin, ungiform, with nail.

Coxae 1-3 distinctive, elongate and with several moderate setae on the posterior half of their medial faces, ventral margins sparcely set with short setae, the posteroventral seta emerging from a small notch; coxa 4 with posterior lobe, excavate; anterior lobe of coxa 6 not produced, ventral margin of coxa 6 without spines. Gnathopods slender, not eusirid, with subchelate oblique palm; segment 5 of gnathopod 2 longer than segment 6 in female; gnathopod 2 of male not enlarged, palm with less than 4 barb spines in the outer row.

Dactyls of peraeopods 3-7 non-castellate, with 2 small setae near the uncinus; segment 2 of peraeopods 3 and 4 not anteriorly lobate; peraeopod 5 nearly as long as peraeopod 7; segment 2 of peraeopods 5-7 very broad, subcircular, posteroventrally lobate, that of peraeopod 7 with a posterodorsal lobe; segment 5 of peraeopods 5-7 shorter than segment 6.

Pleopods ordinary; pleopod 2 of male gonopodous. Posteroventral corner of epimeron 2 acutely produced; epimeron 3 with 1-3 shallow posterior notches. Peduncles of uropods 1 and 2 not dorsally broadened; rami of uropod 1 subequal; outer ramus of uropod 2 shorter than inner ramus. Uropod 3 extending beyond uropod 1; peduncle without a large process; rami equal in length, narrow, lanceolate, with plumose setae. Lobes of telson fused less than a quarter of its length, apical margins tapered or notched, with 2 or more

setae.

Coxal gills present on peraeopods 2-6 in both sexes; gills moderate but shorter than anterior coxae. Sternal gills absent. Female with large oostegites on peraeopods 2-4 and a smaller strap-like oostegite on peraeopod 5; oostegite of peraeopod 2 narrow, not wider than this coxa.

Relationships. The subgenus *Moanamoera* is like the grade "*Paramoera*" (defined above), but differs in the reduced and unpigmented eye, the lack of a cleft in the inferior antennal sinus, the short segment 3 of the mandibular palp, the elongate and medially setose coxae, the broadly subcircular segment 2 of peraeopods 5-7, and the acutely produced corner of epimeron 2. It differs from *Paramoerella* Ruffo, 1974, in the short segment 3 of the mandibular palp, the elongate and medially setose coxae, the broadly subcircular segment 2 of peraeopods 5-7, and the acutely produced corner of epimeron 2. *Moanomoera* also differs from *Relictomoera* Barnard & Karaman, 1982, in the mammilliform (non-sinusoid) anterior margin of the head; from *Sternomoera* Barnard and Karaman, 1982, in the absence of sternal gills; and from *Pseudomoera* Schellenberg, 1929, in the more typical (non-geniculate) segment 5 of the gnathopods. *Moanomoera* is similar to *Humilomoera*, n. s-g., in the uncleft inferior antennal sinus, and in the reduced, unpigmented eye, but differs from it in the greater setosity of maxillae 1 and 2, the longer and medially setose coxae, the absence of spines from coxa 6, the acutely produced corner of epimeron 2, and the plumose third uropod. Moanomoera differs from *Rhithromoera*, n. s-g., in the nearly equal antennae, the setae of the gland cone, the shorter segment 3 of the mandibular palp, the slender gnathopods (with elongate segment 5 in gnathopod 2 of female), the broadly subcircular segment 2 of peraeopods 5-7, the more acutely produced epimeron 2, and the plumose rami of uropod 3.

Species. *Paramoera (M). rua* J. L. Barnard, 1977; *P. (M). paakai* J. L. Barnard, 1977; *P. (M). lokowai* J. L. Barnard, 1977; from the Hawaiian Islands; in brackish ponds, cave pools, and groundwater.

Etymology. From the Hawaiian word *moana* (= deep blue sea), denoting isolation in the open ocean, and *moera*, implying alliance to related genera with the same root.

Paramoera (Moanamoera) rua J. L. Barnard, 1977

Paramoera rua J. L. Barnard, 1977: 275-282, figs. 7, 8, 9 (part).

Material examined.
Hawaii: Waianapanapa Cave, Hana, Maui Island (20°45'N, 156°00'W), 24 January 1973, collected by ELB and FGH from a brackish cave pool (4 specimens).

Diagnosis. Eye poorly developed and unpigmented;

antennal sinus shallow, without a cleft; antenna 1 only slightly longer than antenna 2; major peduncular segments of antennae with about 3 groups of short setae along the ventral margins; gland cone with 2-3 moderate setae.

Inner plate of maxilla 1 with 8-10 plumose setae; inner plate of maxilla 2 with 5 plumose setae.

Segment 6 of gnathopod 1 with about 4 posterior groups of comb setae, palm with 2 outer and 2 inner barb spines; segment 6 of gnathopod 2 with 5 posterior groups of comb setae and with sparce medial setae; gnathopod 2 of female with segment 5 about 25% longer than segment 6; gnathopod 2 of male with segment 5 nearly as long as segment 6, palm oblique, palm about 50% as long as the posterior margin.

Posterior margin of segment 6 of peraeopod 4 with 5 ornamental groups, each consisting of a single barb spine and a seta on its lateral side (distal spines accompanied by additional setae); posterior margin of segment 2 of peraeopod 7 with shallow notches, segment 4 about 25% as wide as segment 2, longest spines of segment 5 about 60% as long as the dactyl, longest spines of segment 6 about 60% as long as the dactyl.

Posteroventral corner of epimeron 2 acute but poorly produced; posterior margin of epimeron 3 with 2-3 shallow notches, posteroventral corner angular but without a significant tooth; peduncle of uropod 1 with 7 dorsolateral spines; uropod 2 with shortened outer ramus; uropod 3 with plumose setae; telson fused about 10% its length, each apex notched, with 3-4 long setae.

Coxal gills on peraeopods 2-6 (lacking on pereopod 7).

Examination of the material. Little can be added to J. L. Barnard's (1977) well illustrated description of this species. The specimens examined in the present study lacked a gill on peraeopod 7 in both sexes. The oostegites are of the narrow form (cf. "*Paramoera*"). A 4.5 mm male possessed a single posterior calceolus on alternate segments 5-15 and a single medial calceolus on alternate segments 6-12 (absent from the peduncle) of antenna 1; antenna 2 lacking both calceoli and aesthtascs. Pleopod 2 is gonopodous in the male.

Size range. Both sexes to about 5 mm.

Color in life. Unknown.

Distribution. Known only from the type locality on Maui, Hawaiian Islands.

Ecology. *Paramoera (M.) rua* is found in a brackish cave pool under low light conditions. Its biology is unknown, but the absence of filtering setae on the antennae suggests that this species is primarily a detritivore, using the ventral and medial setae of the gnathopods to gather and process detrital/ bacterial deposits. A single female in this collection was brooding six eggs, indicating a low fecundity. The salinity at the collecting site ranged from 2 to 4 ppt.

Remarks. The three Hawaiian species described by J. L. Barnard (1977) share many derived characters (see diagnosis of *Moanamoera*, n. s-g.). They form a closely related group,

termed a "geminate triad" by Barnard, which clearly evolved from a common ancestor. In the subsequent analyses and discussion I have lumped these three species as *Paramoera (Moanamoera)* spp.

Paramoera (M.) rua differs from *P. (M.) lokowai* J. L. Barnard, 1977, by the presence of eyes, by the shorter peraeopods, and by the shorter rami of uropod 3; it differs from *P. (M.) paakai* J. L. Barnard, 1977, by the setae (not spines) of the epimera, by the reduced fusion of the telson, and by the deep apical notches of the telson.

The material examined differs slightly from the original description of *P. (M.) rua*, and was termed "variant" by Barnard (1977, p. 279). These specimens possess reduced eyes and atypical ornamentation of the antennna and mandible. I have not examined sufficient material of both forms to confirm Barnard's suggestion that this constitutes a new species.

Paramoera (Humilomoera), new subgenus

Type species. *Paramoera (Humilomoera) leucophthalma*, new species.

Diagnosis. Rostrum unproduced; lateral cephalic lobe mammilliform; inferior antennal sinus shallow and without a cleft. Eye reduced, round, with or without pigment. Antennae of moderate length, antenna 1 longer than antenna 2; peduncular segments of antenna 1 progressively shorter, segment 1 shorter than the head; accessory flagellum 1-segmented, scale-like; ventromedial setae of peduncles short; gland cone with a single short seta; calceoli present only in male.

Upper lip entire and rubrounded; epistome unproduced. Molar triturative, oval; palp segment 2 equal to or slightly longer than segment 3; lower lip without distinct inner lobes. Maxilla 1: inner plate with 3-4 plumose setae, outer plate with 10-11 pectinate spines; palp long, segment 1 short. Maxilla 2: inner plate with a submarginal row of 2 plumose setae. Maxilliped: inner plate about as long as outer, outer plate with less than 4 medial spine teeth; palp of 4 segments, segment 1 not laterally extended, segment 3 unlobed, segment 4 shorter than segment 3, segment 4 not spinose (but with small distal setae) along the inferior margin, ungiform, with nail.

Coxae 1-3 ordinary (neither anteriorly nor ventrally produced), sparcely setose, the posterior seta slightly enlarged; coxa 4 with posterior lobe, excavate; anterior lobe of coxa 6 small to moderate in size, ventral margin of coxa 6 with spines. Gnathopods feeble, not eusirid, with subchelate oblique palm; segment 5 of gnathopod 2 subequal to or longer than segment 6 in female; gnathopod 2 of male not enlarged, palm with less than 4 barb spines in the outer row.

Dactyls of peraeopods 3-7 non-castellate, with 2 small setae near the uncinus; segment 2 of peraeopods 3 and 4 not anteriorly lobate; peraeopod 5 about 80% as long as peraeopod 7; segment 2 of peraeopods 5-7 expanded and ovate, posteroventrally lobate; segment 5 of peraeopods 5-7 shorter than segment 6.

Pleopods ordinary; pleopod 2 of male gonopodous. Posteroventral corner of epimeron 2 not acutely produced; epimeron 3 with 2 posterior notches, the posteroventral corner with a small recurved tooth. Peduncles of uropods 1 and 2 not dorsally broadened; rami of uropod 1 subequal; outer ramus of uropod 2 shorter than inner ramus. Uropod 3 extending beyond uropod 1 (hardly so in *P. (H.) crassicauda*); peduncle without large process; rami equal in length, narrow, lanceolate, without plumose setae, but with a single simple setae on the outer margin of the outer ramus. Lobes of telson variously fused (more than half the length in *P. (H.) crassicauda*), each apex rounded, with 2 apical setae.

Coxal gills present on peraeopods 2-6 in both sexes, anterior gills reduced in female. Sternal gills absent. Female with large oostegites on peraeopods 2-4 and a smaller strap-like oostegite on peraeopod 5; oostegite of peraeopod 2 proximally broadened and wider than this coxa.

Relationships. Subgenus *Humilomoera* is like the grade "*Paramoera*" (defined above), but differs in the smaller (occasionally unpigmented) eye, the lack of a cleft in the inferior antennal sinus, the reduced ornamentation of the gland cone, the reduced setosity of maxillae 1 and 2, the less setose antennae, and the reduced gills. The broad oostegites, the spines of coxae 6, and the non-plumose uropod 3 also distinguish this subgenus from most members of "*Paramoera*." *Humilomoera* resembles *Paramoerella* Ruffo, 1974, in the reduced eye, the uncleft inferior antennal sinus, the reduced gills (small, and absent from peraeopod 7), and the non-plumose uropod 3, but differs from that genus by the structure of the accessory flagellum, the reduced setosity of maxillae 1 and 2, the absence of the inner lobes of the lower lip, and the reduced ornamentation of the telson. It differs from *Relictomoera* Barnard & Karaman, 1982, by the mammilliform (non-sinusoid) anterior margin of the head; from *Sternomoera* Barnard & Karaman, 1982, by the absence of sternal gills; and from *Pseudomoera* Schellenberg, 1929, by the more typical (non-geniculate) segment 5 of the gnathopods. *Humilomoera* is similar to *Rhithromoera*, n. s-g., in the small eye, the uncleft inferior antennal sinus, the reduced setosity of the antennae and maxillae, and the non-plumose uropod 3, but differs in the shallow depth of the inferior antennal sinus, the more feeble gnathopods, the reduced gills, the ventral spines of coxa 6, the shorter segment 5 of peraeopods 5-7, the reduced serration of epimeron 3, and the less setose telson. It is similar to *Moanamoera*, n. s-g., in the uncleft inferior antennal sinus and the reduced (occasionally unpigmented) eye, but differs in the reduced setosity of maxillae 1 and 2, the shorter coxae, the ventral spines of coxa 6, the unproduced corner of epimeron 2, and the non-plumose uropod 3.

Species. *Paramoera (H.) leucophthalma*, n. sp.; *P. (H.) crassicauda*, n. sp.; eastern North Pacific, from Alaska to Washington; in gravel and cobble substratum, ranging from marine subtidal to freshwater streambeds.

Etymology. Latin: *humilo* = humble, suggesting a reduction of many characters, and *moera*, implying alliance to related genera with the same root.

Paramoera (Humilomoera) leucophthalma, new species
(Figs. 7A, 7B)

Paramoera leucophthalma Staude, 1986: 117-131, figs. 1.13 and 1.14.
"*Paramoera leucophthalma* Staude (in press)" of Staude 1987: 376 and 378.

Material examined.
Barkley Sound, British Columbia, off north shore of Cape Beale (48°48.0'N, 125°12.0'W), NMC Station B20, 5 July 1976, collected by ELB and FR aboard R/V LEIK, dredged at 30 m, in gravel and among small stones.
Holotype: female, NMC-IZ1986-055; allotype, male, NMC-IZ1986-055; 23 paratypes NMC-1976-157.

Additional material.
BRITISH COLUMBIA: Barkley Sound, British Columbia, off north shore of Cape Beale (48°48.2'N, 125°11.3'W), NMC Station B21, 5 July 1976, collected by ELB and FR aboard R/V LEIK, dredged at 20-22 m, in gravel (1 specimen); off Bordelais Islet (48°48.5'N, 125°14.0'W), 5 July 1976, collected by ELB and FR aboard R/V LEIK, dredged at 42 m in gravelly sand (1 specimen).

Diagnosis. Eye small and unpigmented; inferior antennal sinus shallow, without a cleft; antenna 1 about 40% longer than antenna 2; segment 1 of antenna 1 with a single distoventral spine; major peduncular segments of antennae with about 3 sparse groups of short setae along the posterior margins; gland cone with a single small seta.

Mandibular palp with an unusually large plumose seta at the distal end of segment 2; inner plate of maxilla 1 with 4 plumose setae; inner plate of maxilla 2 with 2 plumose setae near the inner margin.

Segment 6 of gnathopod 1 with 3-4 posterior groups of comb setae; segment 6 of gnathopod 2 with 5-7 posterior groups of comb setae and with sparse medial setae; gnathopod 2 of female with segment 5 about 10% longer than segment 6; gnathopod 2 of male with segment 5 about 75% as long as segment 6, palm oblique and about 50% as long as the posterior margin.

Posterior margin of segment 6 of peraeopod 4 with 2-3 ornamental groups, each consisting of a single barb spine and a curved seta on its lateral side (the distalmost spine accompanied by long setae); posterior margin of segment 2 of peraeopod 7 moderately serrated, segment 4 about 35% as wide as segment 2, spines of segments 5 and 6 not longer than 60% of the length of the dactyl.

Posterior margin of epimeron 3 with 2 distinct notches, the notch at the posteroventral corner bounded by a small tooth; uropod 3 without plumose setae; each apex of telson with a very slender spine and a plumose seta.

Coxal gills of peraeopods 2-4 reduced in female; both sexes lacking a gill on peraeopod 7.

Size range. Not exceeding 4 mm.

Color in life. Unknown.

Distribution. Known only from Barkley Sound, British Columbia (latitude 49°).

Ecology. *Paramoera (H.) leucophthalma* is found interstitially in subtidal gravel, occurring deeper than any other related (*Paramoera* and allied genera) species of this region. The absence of filtering setae on the antennae suggests that this species is primarily a detrital deposit feeder. Its fecundity (2-3 eggs per brood) is notably low. Temperature at the collecting localities was about 8.0°C, and the salinity exceeded 33 ppt.

Remarks. *Paramoera (Humilomoera) leucophthalma* resembles *P. (H.) crassicauda*, n. sp., in the many character states of reduction, typical of the subgenus. It may be distinguished from that species by the unpigmented eye, the distal spine of segment 1 of antenna 1, the uniform setae of segment 3 of the mandibular palp, the more setose gnathopods, the longer carpus of gnathopod 2 of the female, the narrower bases of the posterior peraeopods, the more spinose ventral margins of the epimera, the smaller peduncular spines of the uropods, the shorter outer ramus of uropod 2, the longer rami of uropod 3, and the deeper cleft of the telson. The unpigmented eye, the shallow and uncleft inferior antennal sinus, the slightly shortened segment 3 of the mandibular palp, and the elongate female carpus of gnathopod 2 are similar to the characters of the Hawaiian subgenus *Moanamoera*. The gland cone, the elongate carpus of the female gnathopod 2, the third epimeron, and the telson bear resemblance to *P. bousfieldi.*, n. sp. The distinctly serrate basal segments of peraeopods 5-7 and the sculpture of epimeron 3 are similar to those of *P. serrata*, n. sp.

Etymology. This species name (Gr. *leukos* white + *ophthalmos* eye) refers to the unpigmented nature of the eye. This name was proposed by Dr. E. L. Bousfield (unpublished) who used it as a provisional name in some NMC records.

Paramoera (Humilomoera) crassicauda, new species
(Figs. 8A, 8B)

Paramoera crassicauda Staude, 1986: 132-142, figs. 1.13 and 1.15.

Material examined.
Steamer Bay, Etolin Island, Alaska (56°8.0'N, 132°40.0'W), summer 1981, collected by M.M. from cobble sediment in the tidal reach of Porcupine Creek.
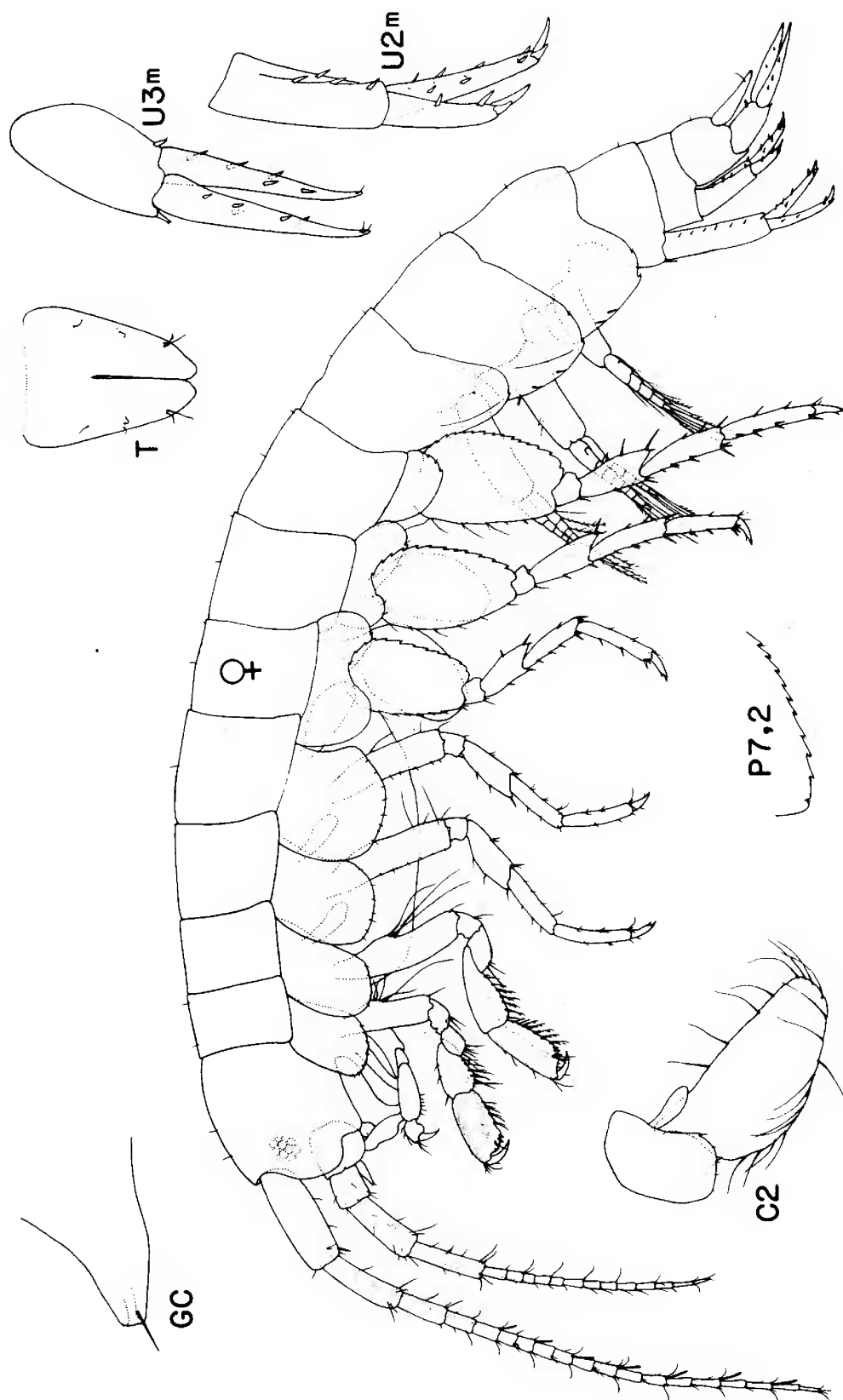
FIG. 7A. *Paramoera (Humilomoera) leucophthalma*, n. sp.; holotype female (3.6 mm); m = allotype male (3.0 mm); Barkley Sound, British Columbia.
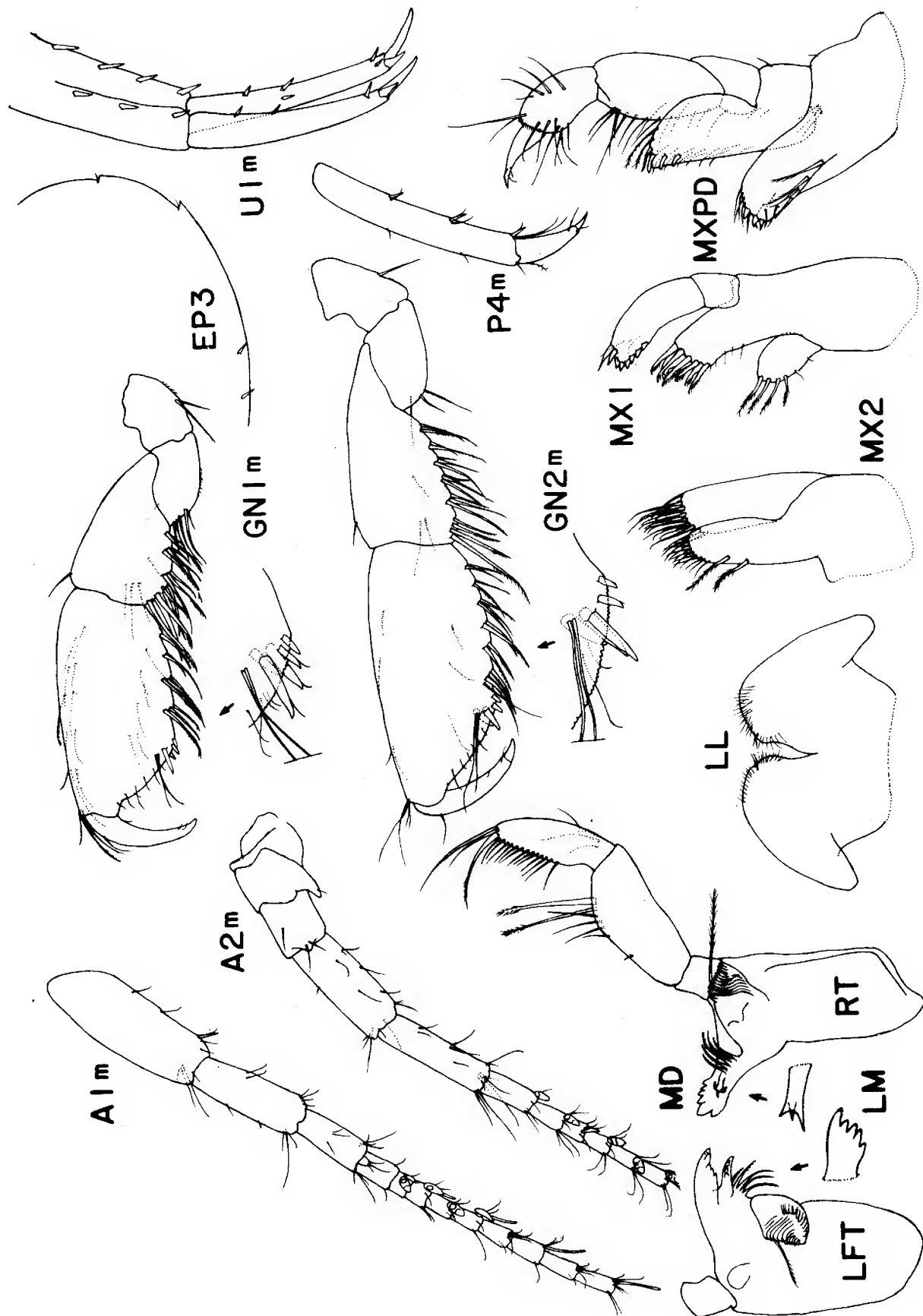
FIG. 7B. *Paramoera (Humilomoera) leucophthalma*, n. sp.; holotype female (3.6 mm); m = allotype male (3.0 mm); Barkley Sound, British Columbia.

Holotype. female, USNM-231322 (1 specimen).

Diagnosis. Eye small, pigmented; antennal sinus without cleft; antenna 1 longer than antenna 2; major peduncular segments of antennae with 2-3 sparse groups of short setae along the ventral margins; gland cone with a single small seta.

Mandibular palp with enlarged pectinate setae at the distal end of segment 2; inner plate of maxilla 1 with 3 plumose setae; inner plate of maxilla 2 with 2 plumose setae near the inner margin.

Segment 6 of gnathopod 1 with 2 posterior groups of comb setae; segment 6 of gnathopod 2 with 3 posterior groups of comb setae and with sparse medial setae; gnathopod 2 of female with segment 5 about 90% as long as segment 6, palm oblique and about 50% as long as the posterior margin; posterior margin of segment 6 of peraeopod 4 with 3 spines, the central spine with a curved seta on its lateral side and the distalmost spine with 2 long setae.

Posterior margin of segment 2 of peraeopod 7 moderately serrated, segment 4 about 32% as wide as segment 2, spines of segments 5 and 6 not longer than 60% of the length of the dactyl.

Posterior margin of epimeron 3 with 2 distinct notches, the notch at the posteroventral corner bounded by a small tooth; rami of uropod 3 about as long as peduncle, uropod 3 without plumose setae; telson with lobes fused about 70% of its length; each apex of telson with a stout seta and a small plumose seta.

Coxal gills reduced; female lacking a gill on peraeopod 7. (male unknown)

Size range. Not exceeding 4 mm.

Color in life. Unknown.

Distribution. Known only from Steamer Bay, Alaska (latitude 58°N).

Ecology. *Paramoera (Humilomoera) crassicauda* occurs among cobbles and gravel in the tidal reach of streams. The absence of filtering setae on the antennae suggests that this species is primarily a detrital deposit feeder. Water temperature at the collecting locality reached a summer maximum of 20°C; the salinity ranged from 1 to 28 ppt (Murphy, 1984).

Remarks. *Paramoera (Humilomoera) crassicauda* shares with *P. (H.) leucophthalma* n.sp. the distinctive reduced characters of this subgenus (see remarks under *Humilomoera*). Yet it differs from that species by the pigmentation of the eye, the lack of a distal spine on segment 1 of antenna 1, the more irregular setae of mandibular palp segment 3, the less setose gnathopods, the shorter carpus of gnathopod 2, the distally broader bases of the posterior peraeopods, the less spinose epimera, the larger spines of the peduncles of uropods 1 and 2, the enlarged subapical spine of the inner ramus of uropod 1, the longer outer ramus of uropod 2, the shortened rami of uropod 3, the fused nature of the telson, and the smaller gills

of peraeopods 5 and 6. The reduced anterior gills of both species are perhaps a concession to increased brood space in these small-bodied species. The short rami of uropod 3 of *P. (H.) leucophthalma* are unique among North Pacific *Paramoera*, but resemble those of *P. hurleyi* Thurston 1972. Similarly the fused telson is unknown in northern species, but is like that of the Antarctic *P. walkeri* (Stebbing, 1906).

Etymology. This species name refers to the unique condition of the telson in which the lobes are fused for more than half their length. It is derived from the Latin *crassus*, meaning "that which has grown or increased" (solid or thick), and *cauda*, meaning tail.

Rhithromoera, new subgenus

Type species. *Paramoera carlottensis* Bousfield, 1958.

Diagnosis. Rostrum unproduced; lateral cephalic lobe mammilliform; inferior antennal sinus deep and angular but without a cleft. Eye reduced, round or oval, pigmented.

Antennae elongate, antenna 1 much longer than antenna 2, peduncular segments of antenna 1 progressively shorter, segment 1 shorter than the head; ventromedial setae of peduncles short and thickened; accessory flagellum 1-segmented, scale-like; gland cone with a ventrally deflexed spine; calceoli present only in male.

Upper lip entire and subrounded; epistome unproduced. Molar triturative, tall, and narrow [similar to Ueno's (1971a) figure of *Relictomoera relicta*]; palp segments 2 and 3 of subequal length; lower lip without distinct inner lobes.

Maxilla 1: inner plate with 4-5 plumose setae, outer plate with 10-11 pectinate spines; palp long, segment 1 short. Maxilla 2: inner plate not broader nor longer than outer plate, inner plate with a submarginal row of 3 plumose setae. Maxilliped: inner plate about as long as outer, outer plate with 3 or more medial spine teeth; palp of 4 segments, segment 1 laterally extended (its lateral margin nearly as long as that of segment 2), segment 3 unlobed, segment 4 shorter than segment 3, segment 4 not spinose (but with small distal setae) along the inferior margin, unguiform, with nail.

Coxae 1-3 ordinary (neither anteriorly nor ventrally produced), sparcely setose; coxa 1 with a small spine at the posteroventral corner; coxa 4 with posterior lobe, excavate; anterior lobe of coxa 6 not produced, ventral margin without spines.

Gnathopods robust and subequal in both sexes, not eusirid, with subchelate oblique palm; segment 5 of gnathopod 2 shorter than segment 6 in female, posteriorly lobate; gnathopod 2 of male slightly swollen, palm with more than 4 barb spines in the outer row.

Dactyls of peraeopods 3-7 non-castellate, with 2 small setae near the uncinus; segment 2 of peraeopods 3 and 4 not anteriorly lobate; peraeopod 5 less than 75% as long as peraeopod 7; segment 2 of peraeopods 5-7 expanded and subrectangular, posteroventrally lobate; segment 5 of
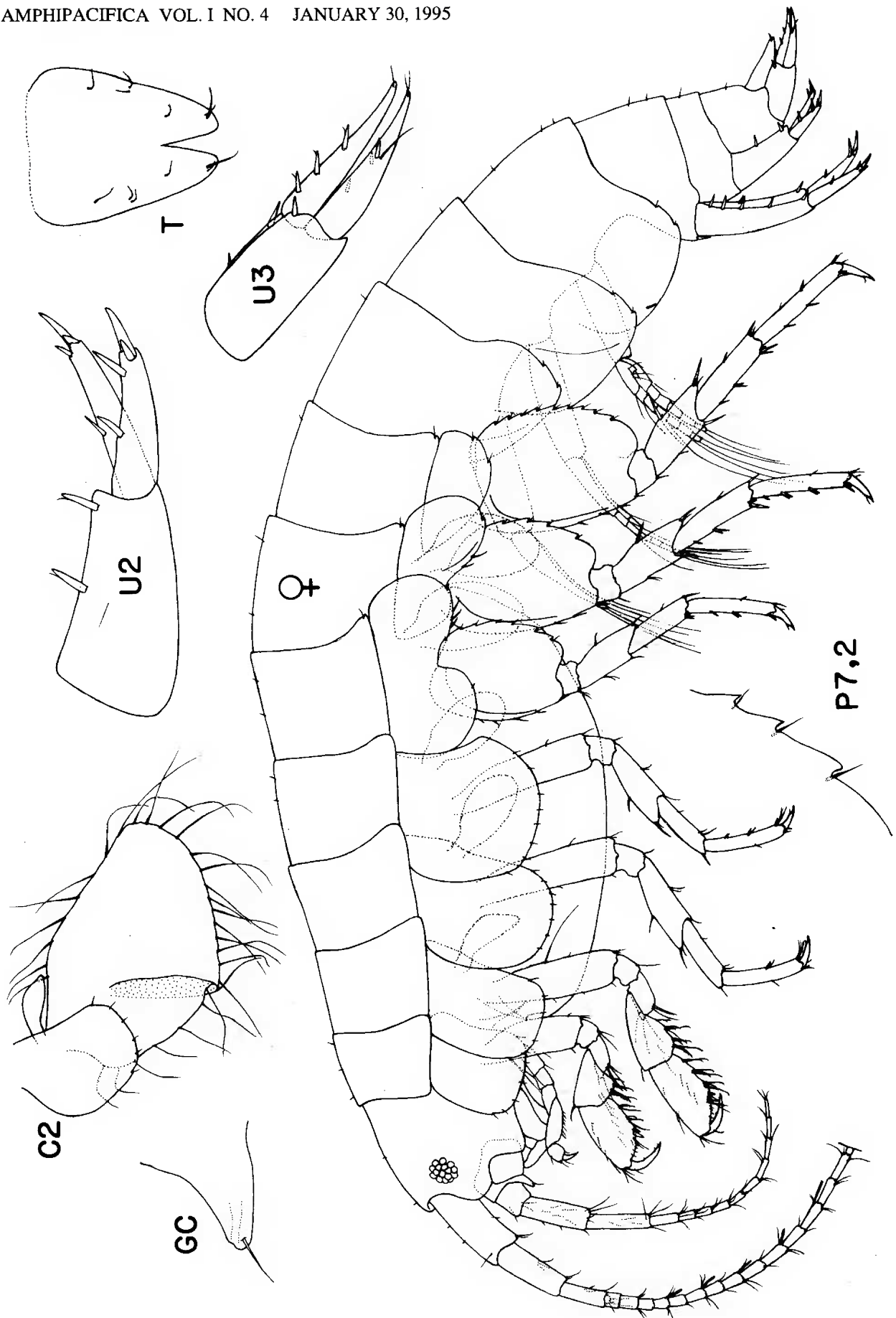
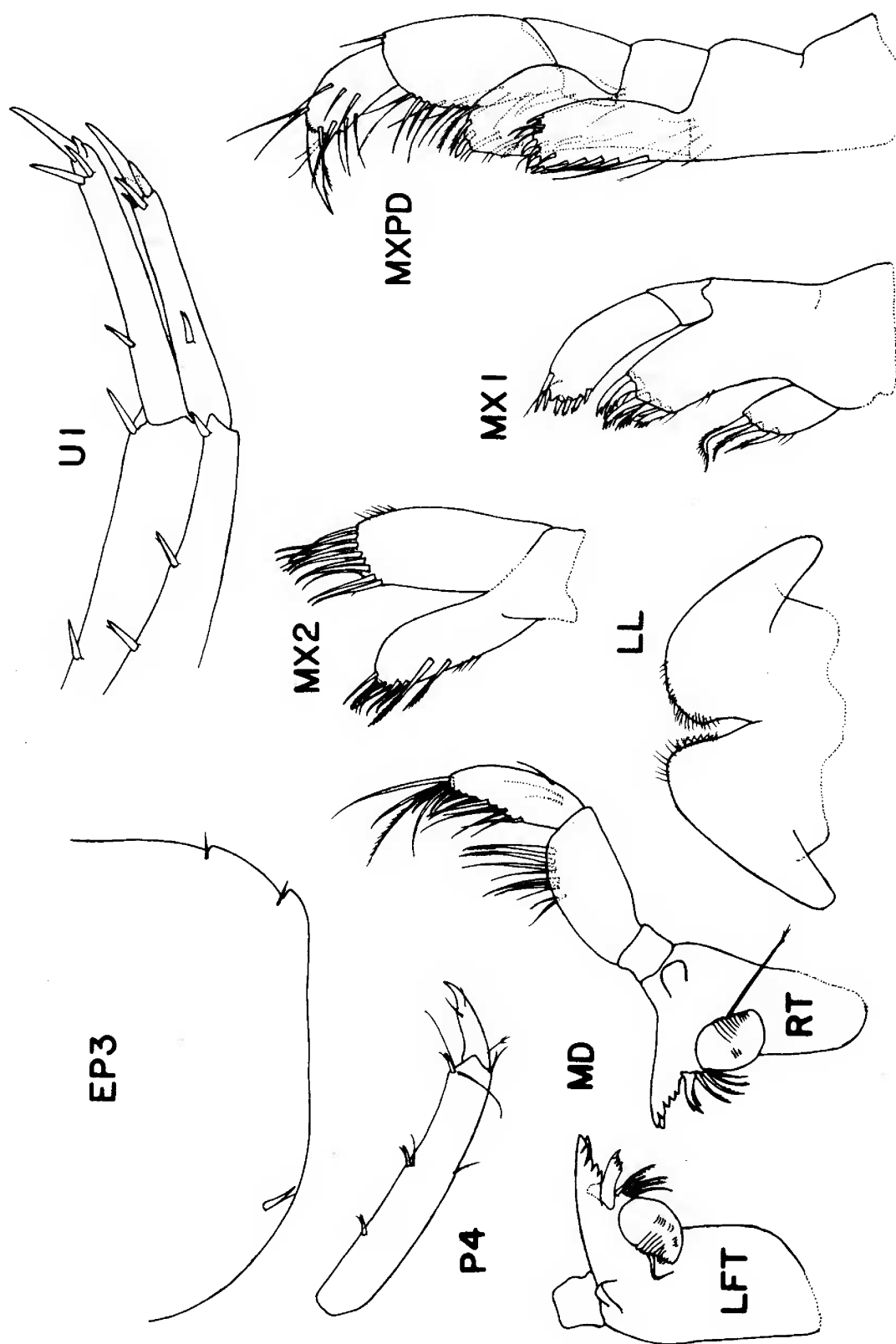**FIG. 8A**. *Paramoera (Humilomoera) crassicauda*, n. sp.; holotype female (3.6 mm). Etolin Island, Alaska.

FIG. 8B. *Paramoera (Humilomoera) crassicauda*, n. sp.; holotype female (3.6 mm). Etolin Island, Alaska.

peraeopods 5-7 not shorter than segment 6. Pleopods ordinary; pleopod 2 of male gonopodous. Posteroventral corner of epimeron 2 not acutely produced; epimeron 3 with 3 or more shallow posterior notches, posteroventral corner without a distinct tooth.

Peduncles of uropods 1 and 2 with broad dorsal surface; rami of uropod 1 nearly equal; outer ramus of uropod 2 shorter than inner ramus. Uropod 3 extending beyond uropod 1; peduncle without large process; rami equal in length, narrow, lanceolate; without plumose setae but with sparce simple setae along the outer margin of the outer ramus.

Lobes of telson fused to half its length, each apex truncate, with a row of 3 or more setae.

Coxal gills present on peraeopods 2-6 and occasionally 7. Female with large oostegites on peraeopods 2-4 and a smaller strap-like oostegite on peraeopod 5; oostegite of peraeopod 2 proximally broadened, wider than this coxa. Sternal gills absent.

Relationships. *Rhithromoera* is like the grade "*Paramoera*" (defined above) but differs in the smaller eye, the lack of a cleft in the antennal sinus, the less setose antennae, the bent spine of the gland cone, the narrower molar, the reduced setosity of maxillae 1 and 2, the short peraeopod 5, the long segment 5 of peraeopods 5-7, the dorsally broadened peduncles of uropods 1 and 2, and the distinctive telson. The broad oostegites and the non-plumose uropod 3 also distinguish this subgenus from most "*Paramoera*".

Rhithromoera differs from *Relictomoera* Barnard & Karaman, 1982, by the mammilliform (non-sinusoid) anterior margin of the head, the bent spine of the gland cone, the short peraeopod 5, the long segment 5 of peraeopods 5-7, the dorsally broadened peduncles of uropods 1 and 2, and the distinctive telson. It differs from *Sternomoera* Barnard & Karaman, 1982, by the bent spine of the gland cone, the reduced setae of maxillae 1 and 2, and the absence of sternal gills.

Rhithromoera differs also from *Pseudomoera* Schellenberg, 1929, by the more typical (non-geniculate) segment 5 of the gnathopods; and from *Paramoerella* Ruffo, 1974, by the reduced setae of the maxillae, and the absence of inner lobes from the lower lip. It is similar to the new subgenus *Humilomoera* by the uncleft inferior antennal sinus, the reduced setosity of the maxillae, and the non-plumose uropod 3, but differs in the deeper inferior antennal sinus, the narrower molar, the bent spine of the gland cone, the more robust gnathopods, the lack of spines on the ventral margin of coxa 6, the more serrate posterior margin of epimeron 3, the larger anterior gills, and the distinctive telson.

Rhithromoera differs from the new subgenus *Moanamoera* in the short antenna 2, the bent spine of the gland cone, the longer article 3 of the mandibular palp, the more robust gnathopods, the shorter segment 5 of gnathopod 2, the narrower segment 2 of peraeopods 5-7, the less acutely produced corner of epimeron 2, and the non-plumose uropod 3.

A deep inferior head sinus and elongate segment 5 of the hind peraeopods are characters shared by many North American taxa within superfamily Gammaroidea (see Bousfield, 1958). However, such similarities are clearly convergent. Species of *Paramoera* and gammaroideans differ markedly in many other characters (e.g., accessory flagellum, maxillae, and uropod 3) that indicate a great phylogenetic distance between these two groups.

Species. *Paramoera (R.) carlottensis* (Bousfield, 1957); *P. (R.) bucki*, new species; eastern North Pacific, from Alaska to Washington; in pools and interstitially in gravel and cobble at the mouths of streams.

Etymology. From the Greek *rhithron*, meaning stream or riverbed, and *moera* implying alliance to related genera with the same root name.

Paramoera (Rhithromoera) carlottensis Bousfield, 1958

Paramoera carlottensis Bousfield, 195: 64-66, fig. 2; Bousfield & Hubbard, 1968: 2?; Staude, 1986: 147-151, fig. 1.16.---Staude, 1987: 376 and 378.

Material examined.
BRITISH COLUMBIA: Stiu Pt., Graham Island (53°14'N, 132°36'W), 26 July 1957, collected by ELB in brackish rock pools at stream mouth (holotype, female; allotype, male; paratypes, 1 female, 10 male/immature; NMC-2279); Gudal Bay, Graham Island (53°13'N, 132°04'W), 27 July 1957, collected by ELB at stream mouth (1 male; NMC-3744).

Diagnosis. Inferior antennal sinus deep and angular, but without a cleft; eye small to medium, dark, oval; antenna 1 about 50% longer than antenna 2; major peduncular segments of antennae with 3-4 groups of short thickened setae along the ventral margins; gland cone with a crooked apical spine and a smaller distomedial spine.

Inner plate of maxilla 1 with 5 plumose setae; inner plate of maxilla 2 with 3 plumose setae.

Segment 6 of gnathopod 1 with 4-5 posterior groups of comb setae, palm with about 6 outer and 4 inner barb spines; segment 6 of gnathopod 2 with 4-5 posterior groups of comb setae and with sparce medial setae; gnathopod 2 of female with segment 5 about 55% as long as segment 6; gnathopod 2 of male with segment 5 about 50% as long as segment 6, segment 6 widest at its midpoint, palm oblique, palm about as long as the posterior margin.

Pposterior margin of segment 6 of peraeopod 4 with 4 ornamental groups, each consisting of a single barb spine and a seta on its lateral side (distal spines accompanied by additional setae); posterior margin of segment 2 of peraeopod 7 with shallow notches, segment 4 about 33% as wide as segment 2, longest spines of segment 5 about 75% as long as the dactyl, longest spines of segment 6 about 60% as long as the dactyl.

Posterior margin of epimeron 3 with 5-6 shallow notches, posteroventral notch without a significant tooth; peduncle of

uropod 1 with 7-8 lateral spines (without an isolated distoventral spine); uropod 2 with shortened outer ramus; uropod 3 without plumose setae, but with a single non-plumose seta on the outer margin of the inner ramus and a small group of non-plumose setae on the outer margin of the outer ramus; telson fused about half its length, each apex truncated, with 3-4 long setae.

Coxal gill of gnathopod 2 reduced (especially in female), both sexes with a moderately large gill on pereopod 7.

Re-examination of the type material. Bousfield (1958) described the inferior antennal sinus of these specimens as "sharply incised." Although this sinus is very angular, the inner corner is minutely rounded and is not cleft.

An obvious "median sternal process" of peraeonite 2 could not be found on any of the type specimens, although the sternum of the holotype does possess a small irregular bump at the anterior margin of peraeonite 1. This does not appear to be a vestigial sternal gill.

Contrary to the original description (but agreeing with Bousfield's Fig. 2), the telson of these specimens is fused for about 50% of its length.

Other material. Alaskan specimens collected by Hubbard in 1965 (Bousfield and Hubbard, 1968) and Bousfield in 1980 (NMC Stations S3B2 and S13B1; Bousfield and Jarrett, 1981) that were originally identified as *Paramoera carlottensis* should be re-examined in light of the description of *P. (R.) bucki*, new species (below).

Size range. Female to about 8 mm; male to about 7 mm.

Color in life. Unknown.

Distribution. Known with certainty from the Queen Charlotte Islands (53°N), and reported from southeastern Alaska (to 61°N).

Ecology. *Paramoera (R.) carlottensis* occurs in low salinity pools at the mouths of streams (temperature = 13°C). Its body is not as compressed as in *R. bucki*; hence it may not share the interstitial burrowing ability of that species. The setae of its antennae are not of the filtering type, but its diet is unknown. No ovigerous females have been collected. The second pleopod of the male is gonopodous.

Remarks. *Paramoera (Rhithromoera) carlottensis* may be distinguished from *P. (R.) bucki* by the larger eye, the distoventral barb spines of segment 1 of antenna 1 and segment 3 of antenna 2, the extra spine of the gland cone, the near absence of proximal setae on segment 2 of the mandibular palp, the additional seta of the inner plate of maxilla 1, and the greater number of blunt spine teeth (9-11 total) on the outer plate of the maxilliped. The gnathopods differ in several respects: *P. (R.) carlottensis* has a shorter carpus (especially in gnathopod 2), a broader propodus (its widest point is just distal to its midpoint), a greater number of posterior setal

groups (especially on gnathopod 1), and a greater number of palmar spines. *P. (R.) carlottensis* also differs by the shorter spines of the posterior peraeopods, the presence of gills on peraeopod 7, the more extensive serration of epimeron 3, the less spinose peduncle of uropod 1 (with shorter apical spines on the rami), the additional simple setae of uropod 3, and the greater fusion of the telson lobes. Furthermore the males of *P. (R.) carlottensis* tend to have more calceoli on the first antenna (including the peduncle).

Paramoera bucki, new species
(Figs. 9A, 9B)

Paramoera bucki Staude, 1986: 152-167, figs. 1.16 and 1.17 "*Paramoera bucki* Staude (in press)" of Staude, 1987: 376 and 378.

Material examined. Deadman Bay, Washington (48°30.7'N, 123°8.7'W), Staude station B, 23 December 1984, collected by C.P.S. in mid-intertidal beach of sandy gravel with buried cobbles in area of freshwater percolation from submergent stream.
Holotype: female, USNM-231323; allotype, male, USNM-231324; 7 paratypes, USNM-231325; 2 paratypes, NMC-IZ1986-055.

Additional material.
ALASKA: Steamer Bay, Etolin Island (56°8.0'N, 132°40.0'W), summer 1981, collected by M.M. from cobble sediment in the tidal reach of Porcupine Creek (7 specimens).

WASHINGTON: Deadman Bay, Washington (48°30.7'N, 123°8.7'W), Staude station B, mid-intertidal beach of sandy gravel with buried cobbles in area of freshwater percolation from submergent stream, April 1983 and January-November 1984 collections of CPS (>20 specimens) and 13 May 1982 collection of ELB and CPS (2 specimens), NMC 1982-251.

Diagnosis. Postantennal sinus without a notch; eye small, dark, and subcircular, antenna 1 about 50% longer than antenna 2; major peduncular segments of antennae with 3-4 groups of thickened setae along the ventral margins; gland cone with a single crooked spine.

Inner plate of maxilla 1 with 4-5 plumose setae; inner plate of maxilla 2 with 3 plumose setae; outer margin of maxillipedal palp segment 1 extending nearly to end of maxillipedal outer plate.

Segment 6 of gnathopod 1 with 3 posterior groups of comb setae, palm with 4 outer and 4 inner barb spines; segment 6 of gnathopod 2 with 5-6 posterior groups of comb setae and with sparse medial setae; gnathopod 2 of female with segment 5 about 80% as long as segment 6; gnathopod 2 of male with segment 5 about 65% as long as segment 6, palm oblique and poorly defined, palm about as long as the posterior margin.

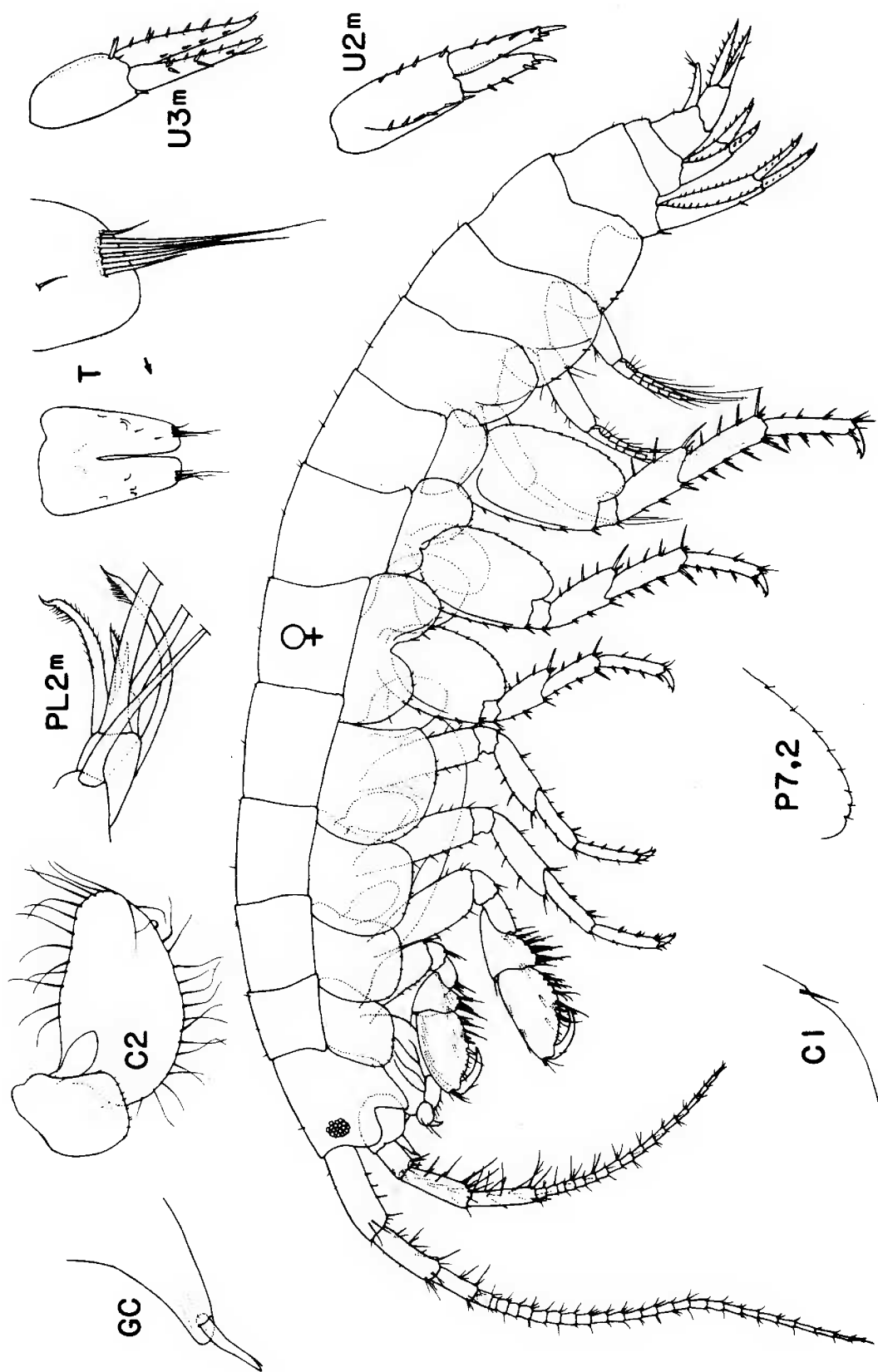Posterior margin of segment 6 of peraeopod 4 with 4

FIG. 9A. *Paramoera (R.) bucki,* n. sp.; holotype female (5.6 mm); allotype male (7.0 mm). San Juan Island, WA.
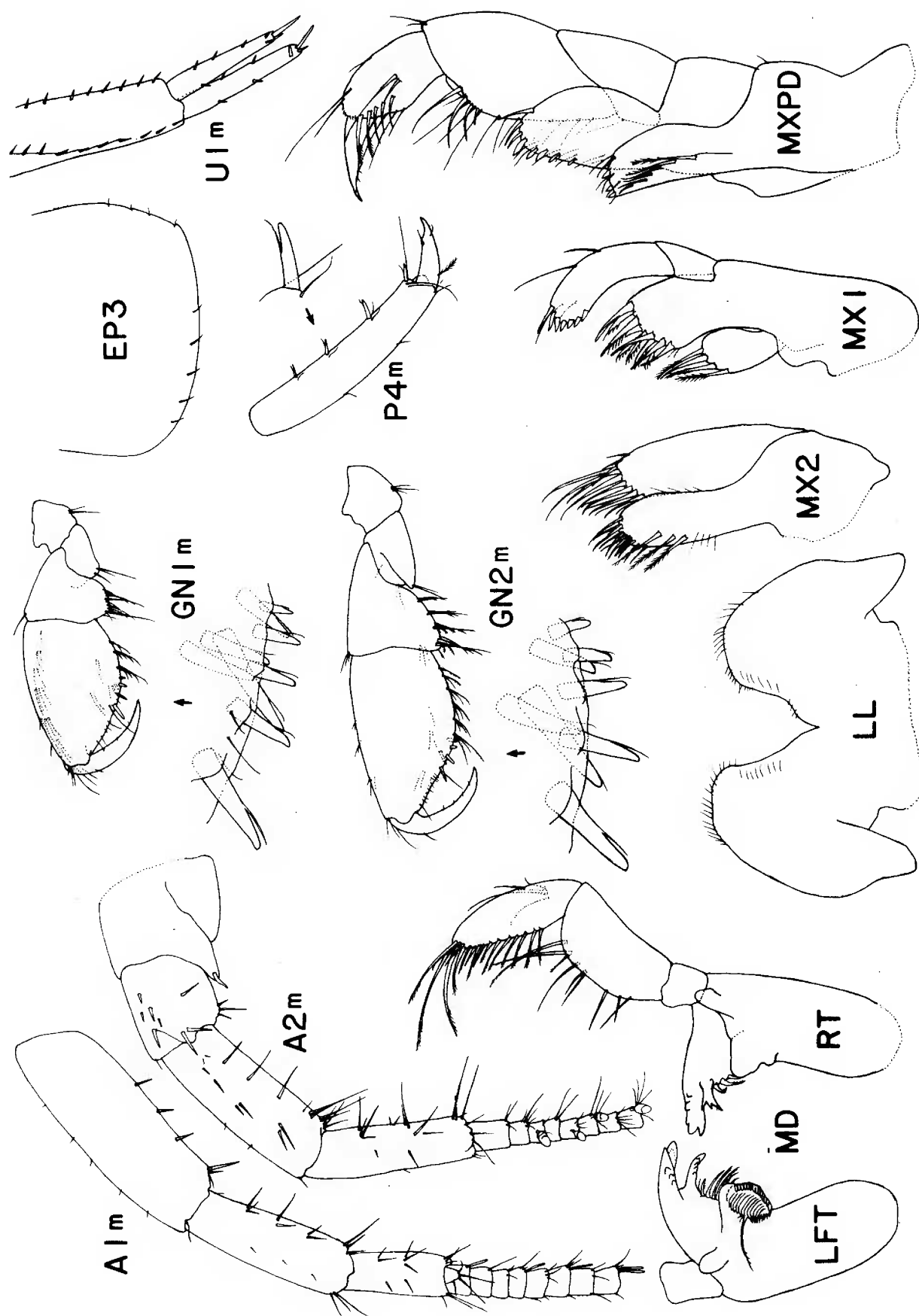
FIG. 9B. *Paramoera (R.) bucki*, n. sp.; holotype female (5.6 mm); allotype male (7.0 mm). San Juan Island, WA.

ornamental groups, each consisting of a single barb spine and a seta on its lateral side (distalmost spine accompanied by long setae); posterior margin of segment 2 of peraeopod 7 with shallow notches segment 4 about 40% as wide as segment 2, longest spines of segment 5 nearly as long as the dactyl, longest spines of segment 6 a-bout 60% as long as the dactyl.

Posterior margin of epimeron 5 with 3-4 shallow notches, posteroventral notch without a significant tooth; peduncle of uropod 1 with 11-13 lateral spines and an isolated distoventral spine; outer ramus of uropod 2 shorter than inner ramus; uropod 3 without plumose setae, but with a single non-plumose seta on the outer margin of the outer ramus; each apex of telson truncated, with 3-4 long setae.

Coxal gill of gnathopod 2 reduced (especially in female); peraeopod 7 lacking coxal gill (both sexes).

Size range. Female to 6 mm; male to 7 mm.

Color in Life. Body translucent pink (without banding), eye black.

Distribution. Known incompletely from southeast Alaska (latitude 56°N) to the San Juan Islands (latitude 48°30'N).

Ecology. *Paramoera (R.) bucki* lives in the tidal reach of streambeds and in intertidal gravel beaches that have considerable freshwater seepage. Its slender body allows it to move interstitially among cobble and gravel particles. Although its antennae and gnathopods are not strongly modified for filtering, the long, stiff, flagellar setae of the second antennae are used to collect and sweep detrital food to the mouth. It could also be conjectured that the spines and stout setae of the antennal peduncles permit the entrapment and restraint of meiofaunal prey, but there is no direct evidence for this assertion. *Paramoera (R.) bucki* can tolerate rapid changes of salinity, from 0 to 32 ppt. Field measurements of salinity range from 0-28 ppt., while temperature measurements range from 8-20°C (Murphy, 1984; and pers. observ.).

Remarks. This species is very similar to *P. (R.) carlottensis* Bousfield, 1958, in sharing the derived characters of the subgenus. *Paramoerabucki* may be distinguished from *P. (R.) carlottensis*, however, by the smaller gill of gnathopod 2, its lack of a gill on peraeopod 7, the fewer blunt spine teeth along the inner margin of the outer plate of the maxilliped, the fewer setae on the third segment of the maxillipedal palp, the relatively longer carpus of the gnathopods, the larger number of spines on the peduncle of uropod 1 (especially the presence of a distoventral spine), and the presence of spines on the distal half of the rami of uropod 1. Additionally, *P. bucki* tends to lack calceoli on antenna 1 of the male, and to have fewer setae on the inner plate of maxilla 1, longer spines on segments 4-6 of peraeopods 5-7, fewer setose notches along the posterior margin of epimeron 3, and to exhibit subtle differences in the ornamentation of uropod 3.

The habitats of these two species are distinct, but may overlap near stream mouths. *Paramoera (R.) bucki* may also co-occur with *P. (H.) crassicauda*. These species are similar in having a small pigmented eye, but *P. bucki* can be distinguished by its deeper inferior antennal sinus, its more robust gnathopods, the longer rami of its third uropod, and by the deep cleft and multiple setae of the telson.

Etymology. This species is named for Mr. Sam Buck, owner of the upland property of Deadman Bay during the author's field studies, and in grateful acknowledgement of his assistance in the author's research performed at Friday Harbor Laboratories.

DISCUSSION

New descriptions.

The six new species of *Paramoera* described here tend to confirm the richness of the overall amphipod fauna of the eastern North Pacific. Bousfield (1981) estimated that this region has more gammaridean species than the western North Pacific or either eastern or western coasts of the North Atlantic. Other taxonomic investigations (e. g., Dickinson, 1982; Conlan, 1983; Jarrett and Bousfield, 1994), involving several other superfamilies, have each revealed a surprising number of previously undescribed species from this coast.

Although the majority of species of *Paramoera* have been described from the southern hemisphere, it is now apparent that this genus is well established in the eastern North Pacific. A total of nine species and one subspecies are here recognized from the west coast of North America and three from the Hawaiian Islands.

Classification.

It is beyond the scope of this work to fully define the genus *Paramoera*. New insights, however, have been gained by examining the eastern North Pacific representatives of this group. It is clear that at least four of these species bear a strong relationship to the "type" form of the sub-Antarctic. In contrast, three new subgenera have been identified that possess apomorphic characters and help to define the evolutionary trends within *Paramoera* as a whole.

The decision to erect these new groups as subgenera was carefully considered. The more common practice has been to erect a full genus for any new species or small flock of species that seem separated by a gap from all known relatives (sensu Mayr, 1969). Examples include the creation of the genus *Paramoerella* Ruffo, 1974, for *P. interstitialis*; the genus *Antarctogeneia*, Thurston, 1974, for *A. macrodactyla*; and the genus *Relictomoera* J.L. Barnard and Karaman, 1982, for *Paramoera relicta* Ueno, 1971 (Ueno, 1971a), and *Paramoera tsushimana* Ueno, 1971 (Ueno, 1971b). This proliferation of small genera within the Pontogeneiidae has been criticized by Shaw (pers. comm.). Barnard & Karaman (1982), elsewhere prolific authors of new amophipod taxa, have

hesitated to add "yet another monotypic genus to the pool."

The subgenera proposed here might make equally valid genera, but for a few considerations. Most important are the matters of scale (cf. Stimpson, 1961) and information content (Wiley, 1981). If we continue the trend of creating a new genus for each distinctly different species or species pair, we belittle the significance of the genus. At the same time we lose information about relationships. Admittedly this is all relative to the higher classification scheme. But since we presently deal with gammarideans only in terms of species, genus, family, and superfamily, any group within *Paramoera* sensu lato that is elevated to generic status loses any obvious alliance to *Paramoera* within the Pontogeneiidae. In the case of *Paramoera*, workers have tried to retain this sense of relationship by maintaining the root "*moera*" in the names of most new descendant genera. Nevertheless, ingenious nomenclature should not be made to compensate for inadequate classification.

The subgenus concept has not enjoyed wide use within the superfamily Eusiroidea. Thurston (1974) and Sagar (1976) have considered the creation of a new subgenus or genus to contain *Paramoera walkeri* (Stebbing, 1906), and J. L. Barnard (1977) suggested that the Hawaiian *Paramoera* might qualify as a new subgenus, but neither has been formally erected. Subgenera were utilized within the old concept of Gammaridae, but this unwieldy group has now been reorganized into new families and full genera (Bousfield, 1977, 1979) and subsequent revisors.

One undeniable advantage of using subgenera for groups within unresolved taxa is the minimal disruption of practical taxonomy (e.g., the use of species lists in environmental surveys) where only the genus and species names are commonly used. This is especially appropriate for *Paramoera*, because further revisions are expected (Shaw, 1984; Thurston, pers. comm.).

The alternative to a subgeneric classification would be to recognize such taxa as genera, but expand the higher categories of the Eusiroidea. For example, a subfamily "Paramoerinae" might be erected to receive *Paramoera* sensu stricto and its allied genera within the family Pontogeneiidae. Such may be the eventual disposition of these new subgenera, as in the case of "good old Gammaridae." But regardless of the exact scheme, future efforts should insure the monophyletic integrity of the component groups. Ideally, the classification should reflect the true pattern of evolutionary descent.

The new subgenera *Rhithromoera* and *Humilomoera* are clearly distinguished by both phenetic and phylogenetic methods (Fig. 10). *Moanamoera* also appears strongly "dissimilar" to the base grade "*Paramoera*" in the phenogram (Fig. 10a). It would have formed a narrowly defined clade in Fig. 10b, if the three species of this subgenus were evaluated as separate taxa. Not only do these subgenera form well defined clusters or clades, but they are distinguished from members of the grade "*Paramoera*" by a dozen or more synapomorphies (enumerated by Staude, 1986). In contrast, the lower branches of the grade "*Paramoera*" are separated by only two or three derived features.

The remaining grade "*Paramoera*" is somewhat of a strawman. It is presently a taxon of convenience, a paraphyletic grade waiting to be revised by subsequent workers. Of its eastern North Pacific members, *P. bousfieldi* is the least congruent; thirteen apomorphies (Staude, 1986) distinguish it from the other members of this group. In the southern hemisphere, *P. walkeri* differs by its poorly setose maxillae, toothed dorsum, and largely fused telson, characters worthy of subgeneric distinction. Other subgenera will become evident as additional species are described and after the known southern species have been redefined.

Evolutionary trends

The fossil record of the Gammaridea is poor (Bousfield, 1982; Bousfield and Shih, 1994) and provides no useful insight into the ancestral state of *Paramoera*. We must therefore look to extant groups to understand the evolution of this genus.

The evolutionary reduction of body parts and ornamentation has been recognized within the Crustacea as a whole by a number of workers (e.g., Sanders, 1963; Bousfield, 1978; Boxshall, 1983; Hessler, 1983). In the Amphipoda the accessory flagellum has long been accepted as a primitive character (J. L. Barnard, 1969a, 1974) that has been lost in the more advanced groups. Within Pontogeneiidae, the fully setose condition of the maxillae has been considered plesiomorphic by J. L. Barnard (1972b) and Thurston (1974). Furthermore, primitive species would be expected to have well developed gills on peraeopod 7 (Bousfield, 1983). These characters are present in the South African species, *Paramoera bidentata* K. H. Barnard, 1932 (see Methods and Fig. 1), which is thought to be close to the ancestral species of *Paramoera*. That is not to say that *P. bidentata* is entirely plesiomorphic; its spinose antennae and toothed pleonites are derived characters.

The presence of calceoli in both sexes of *P. bidentata* (Fig. 1) is a primitive condition at the genus level (cf. Bousfield 1985), but on a larger scale is considered to be derived (Bousfield and Shih, 1994). Calceoli are absent from the female in nearly all other species of *Paramoera* (for a possible exception see J.L. Barnard's, 1972a, Fig. 38 of *P. chevreuxi*). Bousfield (1980; 1985) has observed that calceoli are reduced in the male of some hypogean forms. Indeed, the quasi-hypogean *P. (Rhithromoera) bucki*, often lacks calceoli on antenna 1 of the male. The poorly known males of *Moanamoera* also seem to exhibit a reduction of calceoli. The fine structure of the male calceolus is consistent within the eastern North Pacific *Paramoera* (like that of the male *P. bidentata*, Fig. 1), and is in approximate agreement with the findings of Lincoln and Hurley (1981). It is, however, noteworthy that the calceolus of antenna 1 in the female of the primitive *P. bidentata* is a three-element structure like that of *Gondogeneia* (J. L. Barnard, 1972a, 1972b), while the calceolus of antenna 2 is reduced to a discoid proximal element and a straplike distal element reminiscent of *Amathillopsis australis* Stebbing (Lincoln and Hurley, 1981).

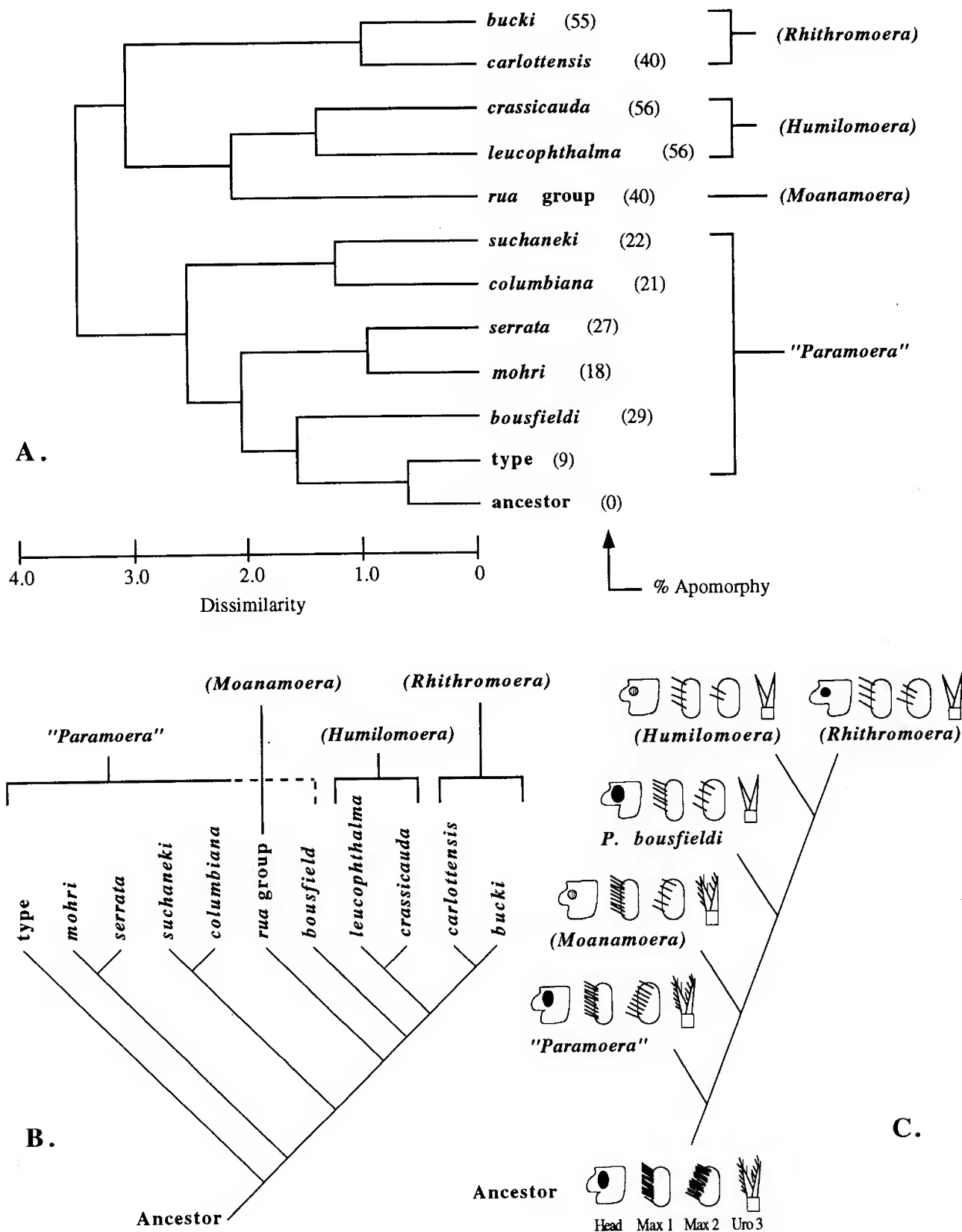The trend in character reduction within *Paramoera* is

FIG. 10. Phyletic analyses of regional species of *Paramoera* compared to the type and ancestral forms based on 52 characters; A. dendrogram produced by phenetic clustering; B. cladogram generated by PHYLIP; C. phyletic diagram of selected characters, which are reduced in the apomorphic subgenera.

schematically illustrated in Fig. 10c. In the more advanced subgenera there is a decrease in eye size and a loss of setae from maxillae 1 and 2. Gills are also reduced in size and lost from peraeopod 7 (illustrated by Staude 1986) in most members of these subgenera. The plumose setae are lost from the third uropod in *Humilomoera* and *Rhithromoera*, and some apomorphic species exhibit partial fusion of the telson lobes.

The ancestral *Paramoera* likely had setose antennae and a full compliment of comblike setal groups on the posterior, medial, and anteromedial surfaces of the gnathopods. Modern species of *Paramoera* utilize these setae as a filtering apparatus to collect suspended particulates from the water column and from the intersitial water within the sediment (Staude, 1986). It does not preclude them from feeding on macroalgae, detrital deposits, or even meiofauna. This feeding-type, perhaps inherited from a proto-crangonyctoid lineage (Bousfield, 1985), probably contributed to the successful radiation of this group. This may have coincided with an increase in plant-derived particulates in the Cretaceous (Bousfield, 1978; Bousfield & Shih, 1994). The more advanced subgenera have forsaken the old ways; their reduced setae are apparently suffient to collect an adequate detrital meal in their present environments.

Concurrent with this reduction of characters has been a general tendency to enter freshwater. Nearly all members of the advanced subgenera are found in fresh or low salinity waters, while the *"Paramoera"* prefer high salinities. Exceptions include *P. (Humilomoera) leucophthalma*, which is a shallow subtidal coastal marine form, and the transitional *P. bousfieldi*, which prefers marine intertidal areas with freshwater seepage. *Paramoera columbiana*, although a member of the grade *"Paramoera,"* is often found in the tidal portion of streams. This penetration into freshwater is also reported for the related Japanese genera, *Relictomoera* and *Sternomoera*, and for *Pseudomoera* in Australia (J. L. Barnard and Karaman, 1982).

Paramoera columbiana also diverges from its congeners by the non-gonopodous second pleopod of the male and the high fecundity of the female. Future investigations of *Paramoera* in other geographic regions should consider these differences in reproductive biology. Examination of the fine structure of the male pleopod 2 and the precopulatory carrying positions (described for *Paramoera mohri* and *P. bousfield* by Staude, 1986, and for *P. columbiana* by Bousfield and Shih, 1994) will provide added clues to the phylogeny of this group. The structure of the gills and the breadth of the oostegites, ignored in all previous descriptions within the genus, have also been shown to be of phylogenetic importance. Although the structure of the calceolus is consistent in eastern North Pacific species, the unique calceoli of the female in *P. bidentata* may help link *Paramoera* to other genera within the Pontogeneiidae.

Biogeography

An estimate of global species richness of *Paramoera* and its allies is presented in Table 3. Although the data (compiled

from many sources, especially J.L. Barnard, 1972a; Thurston, 1974; Bellan-Santini and LeDoyer, 1974; Lowry and Bullock, 1976) suffer from uncertain identifications and unresolved synonomies, some general trends can be observed.

The area of greatest species richness is the region of the Antarctic Penninsula (West Antarctica) through the Scotia Ridge to Tierra del Fuego. The eastern sub-Antarctic islands (i.e., Crozet, Kerguelen, Campbell, Auckland, and Macquarie) taken together are equally rich. Interestingly, many of these southern species are reported over wide ranges. For example, *Paramoera gregaria* (Pfeffer, 1888) has been found at Kerguelen Island (60°E), Macquarie Island (160°E), the Ross Sea (180°E), Cape Horn (65°W), South Georgia (40°W), and Tristan da Cunha (10°W). Whether this apparent low endemism is an artifact of misidentification or the result of a natural phenomenon (e.g., West Wind Drift) cannot be determined at this time.

TABLE 3. Global species richness of *Paramoera* and its closely allied genera.

Region	# spp *Paramoera*/+allies
Eastern North Pacific	9/9
Western North Pacific (Japan)	4/9
Hawaiian Islands	3/3
Eastern tropical Pacific	0?/0?
Western tropical Pacific	0?/0?
Eastern South Pacific	2?/2?
Oceania	0?/0?
Australia	1?/3
New Zealand	2/3
East sub-Antarctic islands	10/10
Scotia Arc/West Antarctic	10/10
East Antarctica	2/2
South Atlantic	4/4
South Africa	1/3
Central and North Atlantic	0/0
Arctic	0?/0?

The six new species of *Paramoera* described here from the eastern North Pacific have elevated the richness of *Paramoera* in the North Pacific to a level only slightly below that of the sub-Antarctic. By considering the closely allied genera, *Relictomoera* and *Sternomoera* of Japan, it can be observed that this species richness is equally balanced on the eastern and western shores of the North Pacific.

South Africa is the home of one of the most primitive species of *Paramoera* (i.e., *P. bidentata*). It appears that most austral *Paramoera* are plesiomorphic (e.g., very setose antennae, maxillae, and gnathopods), although many are known only from sketchy original descriptions. Exceptions include *P. hurleyi* Thurston, 1972, from the South Orkneys; *P. walkeri* (Stebbing, 1906), common in the eastern Antarctic;

and *Pseudomoera gabrieli* (Sayce, 1901) from inland streams of Australia. [Interestingly, a number of other southern pontogeneiid genera (e.g., *Bovallia* Pfeffer, 1888; *Pontogeneiella* Schellenberg, 1929; *Schraderia* Pfeffer, 1888; and *Zaramilla*, Stebbing, 1888) possess fully setose maxillae, but these do not have plesiomorphic counterparts in the northern hemisphere.]

In contrast, many apomorphic groups are found in the North Pacific. The new subgenera *Humilomoera* and *Rhithromoera* display numerous advanced characters (discussed above). The Hawaiian *Moanamoera* and the Japanese *Relictomoera* and *Sternomoera* have moderately setose maxillae, but are apomorphic in many other respects (e.g., reduced eyes, less setose antennae and gnathopods, and sternal gills). Nevertheless, some plesiomorphic taxa may be found on either side of the North Pacific (e.g., *Paramoera koreana* Stephensen, 1944, from Korea and *P. suchaneki* n.sp., from the United States).

Along the west coast of North America there is no clear biogeographic trend in apomorphy. The advanced subgenera, however, are mainly recorded from British Columbia and southeast Alaska, while the relatively plesiomorphic species within the subgenera have been found south of the Strait of Juan de Fuca. This observation contrasts somewhat with the findings of Bousfield (1981), Bousfield and Hendrycks (1994), and Bousfield & Jarrett (1994) whereby the more apomorphic species of talitroidean, pleustid, and phoxocephalid amphipods respectively, tend to be found at lower latitudes along this coast.

Any palaeobiologic explanation of this distributional pattern must be argued without the benefit of fossil information, and for this reason is very speculative. By the criteria of Bousfield (1983), the *Paramoera* lineage is primitive relative to most other gammarideans. Since the origin of the Gammaridea is thought to have occurred in the late Paleozoic (J. L. Barnard & C. M. Barnard, 1982; Bousfield & Shih, 1994), it is concei-able that ancestral *Paramoera* were present in the shallow seas among the microplates of southwestern Gondwana as this supercontinent was breaking up during the Cretaceous Period, about 150-125 m.y. BP (Pielou, 1979; Martin, 1986).

The South African *Paramoera bidentata* might therefore be seen as a plesiomorphic relict, surviving as small populations in restricted intertidal areas of coarse sediment (Griffiths, pers. comm.). Barnard & Barnard (1982) have offered a parallel argument to explain the distribution of freshwater crangonyctins, suggesting that South Africa has drifted into unfavorable latitudes for cold-adapted groups and has become a "dying environment... with some relicts."

The cold waters of Tierra del Fuego and the Antarctic Penninsula might serve as a plausible center of origin from which *Paramoera* has radiated circumpolarly and northward into the Pacific. The paradigm of a "center-of-origin" dominated by plesiomorphic species has been criticized by advocates of vicariance, but Pielou (1979) concedes that some distibutions (Schminke, 1974) are still best explained by this process. Indeed all vicariance hypotheses assume the prior dispersal of the ancestral taxa (Kohn, 1983).

This line of reasoning demands some effective means of dispersal. Sagar (1980; and papers cited therein) states that juveniles of *P. walkeri* migrate offshore. My own observations of *P. mohri* and *P. serrata* (Staude, 1986) have shown that these species make nocturnal excursions into the nearshore plankton. Hence, any arguments that *Paramoera* is an intertidal benthic brooder with poor dispersal potential might be countered. Additionally, J. L. Barnard (1970) emphasized adult rafting as a primary means of amphipod dispersal, a hypothesis supported by the observations of Highsmith (1985). This evidence might be sufficient to explain the diverse sub-Antarctic distribution, by invoking the aid of the West Wind Drift in the Cenozoic to carry amphipods (singly or attached to drift algae) around the southern continent.

The dispersal of *Paramoera* into the North Pacific is harder to explain. Barriers of warm water and unsuitable substratum would seem to block any northward passage, just as *Paramoera* has presumably been barred from the Central and North Atlantic. In jumping this gap, the brachyuran genus *Cancer* is said to have "transgressed the tropics by submergence" (Garth, 1961). *Paramoera*, however, is almost exclusively intertidal in the North Pacific, preferring coarse substrates and an algal/detritus food source; no subtidal representative has been found by intensive sampling off southern California (J. L. Barnard, 1962).

Some temperate species of *Paramoera* will survive for weeks at room temperature (pers. obs.), and the three tropical species from Hawaii provide further evidence that temperature constraints are not insurmountable. Brusca and Wallerstein (1979) concluded that temperature was less important than predation and the presence of suitable substratum in restricting the range of the cold-water isopod genus *Idotea*.

Paramoera walkeri seasonally inhabits the bottom of sea ice (Sagar, 1980), and *P. ?pfefferi* Schellenberg, 1931, occurs on the bouyant blades of the kelp *Macrocystis* (A. Escofet, pers. comm.). Attachment to drifting icebergs or dislodged kelp might have enhanced the success of long range northward dispersal of ancestral species (the former case avoiding the thermal barrier). These mechanisms may have been more likely under the climatic conditions and ocean currents of earlier geological periods.

The penetration of this group into the freshwater epigean and hypogean environments of Japan (evolving sternal gills in the case of *Sternomoera*) suggests a considerable residence time in the North Pacific. Speaking of the North Pacific rim, Bousfield (1981) wrote: "Tectonic movements and crustal upheavals in this region are extensive and frequent, and over the millenia have produced a broad spectrum of intertidal and coastal environments with nutrient rich waters in which an ancient and varied biota has developed." Here periodic outbreaks of gammaridean speciation may have occurred as recently as the Pleistocene (Golikov & Tzvetkova, 1972), spawned by the rapidly changing glacial conditions of this region. Perhaps established in the North Pacific as early as the Mesozoic, the genus *Paramoera* has been subjected to the vicariant effects of these tectonic and glacioeustatic events

for eons, producing the species that we see today.

The presence of this typically cold-water group on the tropical, mid-ocean islands of Hawaii remains anomalous. J. L. Barnard (1977) theorized that these species evolved from a marine ancestor which emigrated from North America or Asia during a cool-water Hawaiian epoch. Although *Moanamoera* does bear affinities to *Humilomoera* spp. and *Paramoera bousfieldi* of western North America, it diverges by many distinctive characters. This argues for a long isolation from all known congeners, and descent from an ancestral type which is now extinct (or undiscovered) elsewhere. The islands of Hawaii and Maui are hardly more than 1 m.y. old, while the islands to the west of the chain increase in age to nearly 70 m.y. (Rotondo et al., 1981). Hence the *Moanamoera* group may have inhabited the Hawaiian-Emperor archipelago for some time, repeatedly island hopping to the younger islands. Bousfield & Howarth (1976) proposed a similar west-to-east colonization of the cave dwelling talitrid amphipods found on Kaui. A continued search for traces of the *Moanamoera* lineage on the older islands of this chain, as well as on more distant island groups, might be very rewarding, offering a test of vicariance hypotheses (e.g., Springer, 1982).

Several authors (Rotondo et al., 1981; Springer, 1982; Kohn, 1983) have proposed that a series of older (>70 m.y.) islands moving north on the Pacific plate from a volcanic hotspot south of the equator was the source of some of the biota presently found on the Hawaiian chain. Similarly, paleontological and geomagnetic evidence (Monger & Ross, 1971; Coney et al., 1980) indicates that some of the Mesozoic terranes which now make up the coast of British Columbia and Alaska also formed at low latitudes and have moved great distances along this coast. Perhaps these too have helped to carry *Paramoera* into the North Pacific, where it survives today as a significant part of the gammaridean fauna.

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